

Systematic Revision of the Genus *Eupleura* H. and A. Adams, 1853 (Gastropoda: Muricidae) in the Neogene to Recent of Tropical America

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Abstract. The systematics of the Neogene to Recent genus *Eupleura* of tropical America are revised, with descriptions of four new species: *Eupleura engerrabunda*, from the Late Miocene of Mexico (Atlantic); *Eupleura gravidentata*, from the Plio-Pleistocene of Colombia (Atlantic); *Eupleura paroudia*, from the Early or middle Pliocene of Mexico (Atlantic); and *Eupleura vokesorum*, from the Pliocene of Costa Rica (Pacific) and Ecuador and the Recent tropical eastern Pacific. Two recent taxa, *Eupleura plicata* and *Eupleura limata*, are also resurrected, increasing the standing diversity of *Eupleura* in the eastern Pacific to seven species. *Eupleura limata*, however, may have become extinct over part or all of its geographic range in historical times with the encroachment of fully marine conditions into its formerly deltaic habitat in the northern Gulf of California.

The southern Caribbean is the site of many important events in the evolutionary history of *Eupleura*. The genus first appears in the Early Miocene fossil record of the southern Caribbean. Additionally, nearly half of the living tropical eastern Pacific species originated in the Caribbean in the Miocene and Pliocene before invading the eastern Pacific through the Central American Seaway. Following closure of the seaway in the Pliocene, however, the genus became extinct in the tropical western Atlantic and is survived today only by species in the tropical eastern Pacific, eastern Gulf of Mexico, and Atlantic coast of North America. Origination of *Eupleura* in tropical America since the Pliocene has occurred only in intertidal habitats of the Gulf of California.

INTRODUCTION

The remarkable preservation and diversity of the late Neogene molluscan faunas of tropical America and their occurrence during a time punctuated by glacial cooling, high amplitude sea-level fluctuations, and a decline in planktonic productivity make their study particularly relevant to understanding the long-term biological impacts of local- and global-scale environmental change (e.g., Stanley, 1986; Vermeij & Petuch, 1986; Allmon et al., 1996a; Jackson & Johnson, 2000; Todd et al., 2002). The systematics of Neogene marine mollusks from tropical America, however, have not been revised for most groups since the faunas were first described (e.g., Woodring, 1928, 1959; Olsson, 1964; Jung, 1965, 1969; and many others). Since this time, intensive sampling efforts have added hundreds of new fossil localities throughout the region, and the material collected will undoubtedly extend the ranges of many species and reveal many others previously unknown to science. Thus, without additional work by specialists, the existing primary literature will remain inadequate for addressing many important aspects of the late Neogene faunal turnover, such as the ecological patterns of species extinctions at the end of the Pliocene and the phylogenetic relationships of species across

the turnover boundary (Allmon et al., 1996b; Jackson et al., 1999; Todd et al., 2002).

The gastropod family Muricidae possesses tremendous taxonomic diversity in tropical America, and its members inhabit a wide range of marine environments and exhibit a diversity of morphological forms and life histories. Such components make them ideal for addressing the environmental, ecological, and morphological controls underlying long-term evolutionary success. E. H. Vokes revised most of the western Atlantic muricid genera previously in a series of monographs (e.g., Vokes, 1989c, 1990, 1992, 1994, 1996; Vermeij & Vokes, 1997), but some of the most species-rich muricid genera in the western Atlantic, including the ocenebrine genus *Eupleura* H. & A. Adams, 1853, have thus far received little treatment. Currently, there is no consensus statement in the literature of the stratigraphic and geographic ranges of the genus *Eupleura*, the standing diversity of living *Eupleura* species in the New World, or the timing and patterns of turnover within *Eupleura* in the Late Neogene.

The present study is a systematic revision of the fossil and living members of the genus *Eupleura* from tropical America. Companion studies, which will be published elsewhere, will review the systematics of the remaining members of the genus *Eupleura* from the subtropical and temperate western Atlantic and investigate the phylogeny of the entire genus using cladistic methods. Preliminary cladistic results (Herbert, submitted) indicate that the sub-

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tropical to temperate western Atlantic species of *Eupleura* are morphologically distinct from the *Eupleura* of tropical America and most likely comprise a monophyletic Pliocene offshoot from a tropical western Atlantic ancestor.

In addition to illustrating type specimens and selecting lectotypes, this study presents new data, including radulae, opercula, shell microstructure, and variability in the morphology of Recent and fossil shells. Most of the fossils examined for this study come from relatively new or unstudied collections, particularly those of the Naturhistorisches Museum Basel and the University of California Museum of Paleontology at Berkeley.

PREVIOUS WORK

Forty species- and subspecies-level taxa have been referred to the genus *Eupleura*, of which 11 have been re-assigned to other genera. These eleven include several taxa from the Paleogene and early Neogene of Europe (i.e., *Ranella alata* Millet, 1854, *Eupleura boutillieri* Cossmann, 1889 [Lozouet et al., 1994]; *Eupleura ogormani* Cossmann, 1923 [Merle, 1989]; *Eupleura subanceps* Cossmann & Peyrot, 1923 [Vokes, 1975]), the Recent of the Indo-Pacific (*Ranella pulchra* Gray in Sowerby, 1836 [Jay, 1839]), the Recent of the eastern Pacific (*Eupleura grippi* Dall, 1911 [Radwin & D'Attilio, 1976; Myers & D'Attilio, 1981]) and the Paleogene to the Recent of the Americas (*Murex morulus* Conrad, 1860 [Vokes, 1970]; *Murex perangulatus* Nomland, 1916 [Hall, 1959]; *Ranella poppelacki* Hornes, 1853 [Petuch, 1987]; *Murex sexangula* Dall, 1915 [Vokes, 1985]; *Eupleura stimpsoni* Dall, 1889 [Vokes, 1970]). Three additional taxa—*Eupleura caudata* var. *crowfooti* (Wood, 1879), from the Pliocene of Great Britain, *Eupleura harbisoni* Richards, 1943, from the latest Oligocene/earliest Miocene of North Carolina, and *Eupleura pterina* Gardner, 1947, from the middle Miocene of northwestern Florida—should be assigned elsewhere (Herbert, in preparation) but have not yet been revised.

The remaining 26 described species and subspecies are correctly assigned to the genus *Eupleura*, although the actual number of distinct species is problematic. All are restricted to the Neogene of the Americas. *Eupleura kugleri* Jung, 1965, which was described from the Early Miocene Cantaure Formation of Venezuela, is the earliest of these species. Several taxa followed in tropical America, including *Eupleura thompsoni* Woodring, 1959, and *Eupleura prenitida* Vokes, 1989, from the Late Miocene Gatun Formation of Panama; *Eupleura olssoni* Vokes, 1989, from the Late Miocene Angostura Formation of Ecuador; and *Eupleura lehneri* Jung, 1969, from the Early Pliocene Melajo Clay of Trinidad. There are no Middle Miocene species recorded in the literature.

The taxonomic status of two Late Pleistocene taxa described from deposits near San Diego, *Eupleura muriciformis* var. *curta* Arnold, 1903, and *Eupleura muriciformis* var. *pleistocenensis* Arnold, 1903, has not been critically evaluated, and it remains unclear whether these should be left as subspecies, elevated to full species status, or synonymized with existing species.

Seven taxa have been described from the Recent fauna of the tropical eastern Pacific: *Eupleura muriciformis* (Broderip, 1833), *Eupleura nitida* (Broderip, 1833), *Eupleura pectinata* (Hinds, 1844), *Eupleura plicata* (Reeve, 1844), *Eupleura triquetra* (Reeve, 1844), *Eupleura muriciformis* var. *limata* Dall, 1890, and *Eupleura muriciformis* var. *unispinosa* Dall, 1890. Of these, most workers accept only *E. muriciformis*, *E. nitida*, *E. pectinata*, and *E. triquetra* as distinct species and consider the remaining three taxa as synonyms of *E. muriciformis* (e.g., Hertlein & Strong, 1955; Keen, 1971; Abbott, 1974; Radwin & D'Attilio, 1976; Vokes, 1984).

There are no species of *Eupleura* in the tropical western Atlantic today, although the genus persists in the subtropical to temperate western Atlantic with three or four species (Herbert, unpublished).

MATERIALS AND METHODS

All specimens referable to *Eupleura* in the type, systematic, and stratigraphic collections of the Academy of Natural Sciences of Philadelphia (ANSP); the California Academy of Sciences in San Francisco (CAS); the Natural History Museum of Los Angeles County—Malacology (LACM); the Natural History Museum of Los Angeles County—Invertebrate Paleontology (LACMIP); the Naturhistorisches Museum Basel, Switzerland (NMB); the Panama Paleontology Project (PPP) at the Naturhistorisches Museum Basel, Switzerland; Tulane University, New Orleans, Louisiana (TU); the University of California Museum of Paleontology at Berkeley (UCMP); the Florida Museum of Natural History at Gainesville—Invertebrate Paleontology and Malacology (UF); and the United States National Museum of Natural History—Paleobiology and Invertebrate Zoology (USNM) were examined for this study. Much of this material was uncatalogued, unsorted, misidentified, and/or had not yet been collected at the time of previous studies of the genus *Eupleura* and, thus, almost certainly was not examined by previous workers. Additional material, including type specimens, was borrowed from the Natural History Museum in London (BMNH), the University Museum of Zoology, Cambridge (UMCZ), the Santa Barbara Museum of Natural History (SBMNH), and the San Diego Natural History Museum (SDNMB). The USGS acronym used herein refers to U.S. Geological Survey localities and corresponds to fossil specimens housed in the USNM.

Locality, stratigraphic, and habitat data were recorded from these collections. Because several thousand lots were examined in all, it is impossible to list detailed locality information for each lot. Instead, these data are provided only for figured specimens, which include ma-

terial representing significant geographic and stratigraphic range extensions presented in this paper.

Radulae were recovered from alcohol-preserved and dried specimens (up to ten per species, when available) by dissolving tissue in a concentrated solution of potassium hydroxide for 24 hr. Radulae were rinsed in a series of hot distilled water washes, and stored in ethanol until prepared for study. Radulae, opercula, shell microstructure samples, and protoconchs were fixed to aluminum tabs, coated with gold (40 nm thickness), and examined with a scanning electron microscope at the Coordinated Instrumentation Facility at Tulane University, New Orleans, Louisiana and the Facility for Advanced Instrumentation at the University of California, Davis.

Stratigraphic correlations for formations and other depositional units follow those used by Jung (1989) and Cotton (1999) or are listed in the discussion section under each species. I follow the Cenozoic chronostratigraphy of Berggren et al. (1995).

Species are treated in alphabetical order below.

SYSTEMATIC DESCRIPTION

Class GASTROPODA Cuvier, 1797

Order NEOGASTROPODA Wenz, 1938

Superfamily MURICOIDEA da Costa, 1776

Family MURICIDAE Rafinesque, 1815

Subfamily OCENEBRINAE Cossmann, 1903

Genus *Eupleura* H. and A. Adams, 1853

Type species: *Ranella caudata* Say, 1822, by subsequent designation, F. C. Baker, 1895.

Description: Shells small to moderately large (20–60 mm). Outline fusiform to globose, with whorls cylindrical or dorso-ventrally flattened. Periphery of body whorl angulate to convex. Protoconch of 1.5–2.5 whorls, smooth, rounded with abrupt, but avariccate, transition into ornamented, juvenile stage. Six to nine teleoconch whorls in adults, bearing eight to fourteen axial lamellae on scalariform, early teleoconch whorls. Axial elements between varices becoming increasingly rib-like to nodulose by penultimate teleoconch whorl. Beginning on fifth or sixth whorl, axial elements forming varices at every fourth to sixth axial and intervarical nodes or ribs in between; varices offset from one another by 180–200°. Varices numbering from two to eight over entire shell. Between six and twelve spiral cords on body whorls with occasional secondaries and tertiaries intercalated between primaries. Aperture narrow to broadly ovate with six denticles on adaxial side of outer lip; columella smooth or covered with irregular rugae. Shallow anal sulcus demarcated by knob or cord at posterior end of columellar wall. Parietal callus narrow, adherent. Siphonal canal narrowly open and gently recurved. Shell color brown, reddish-orange,

purplish-grey, or pure white, with or without broad, simple banding patterns. Shell surface texture smooth, crispate, or scabrous. Presence of intricalx variable. Aperture coloration white, ochre, or deep violet.

Discussion: The genus *Eupleura* was originally described as a subgenus of the cassid genus *Bursa* Röding, 1798 due to the fact that both groups form two varices per single revolution of the shell. Comparative studies of gastropod radulae (Stimpson, 1863), soft anatomy (Carriker, 1981), and egg capsule morphology (D'Asaro, 1991), however, indicate that these shell similarities are the result of convergent evolution, and that *Eupleura* is more closely related to members of the neogastropod family Muricidae.

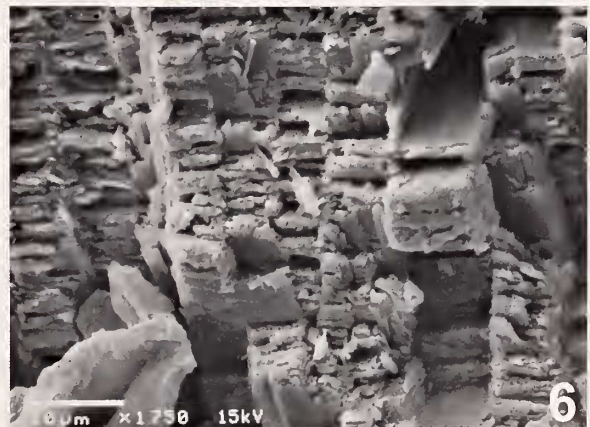
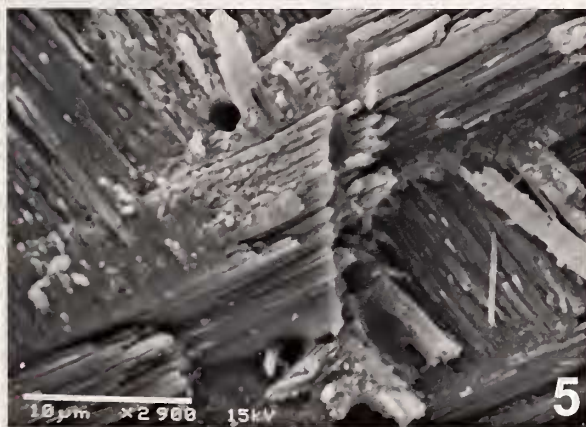
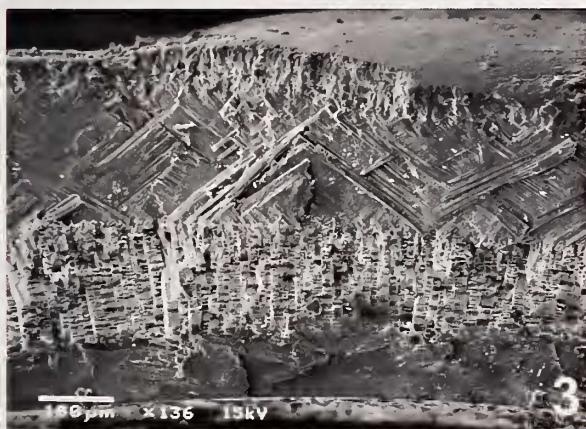
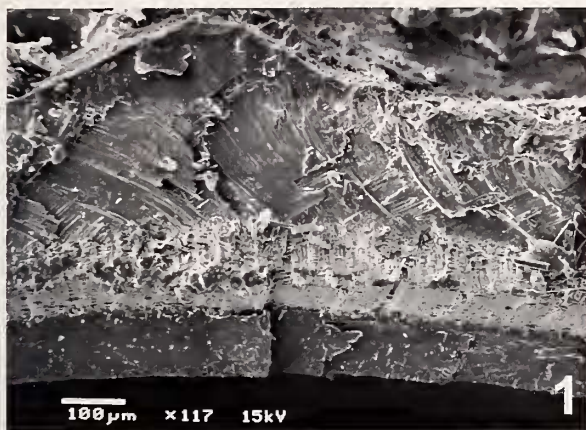
Within the Muricidae, the morphologies of the radulae, opercula, soft anatomy, egg capsules, and shell microstructure of *Eupleura* species are most consistent with the defining characteristics of the subfamily Ocenebrinae (Vokes, 1964, 1971; Radwin & D'Attilio, 1976; D'Asaro, 1991; Kool, 1993a, b; Vermeij & Vokes, 1997; Carriker & Gruber, 1999). These include a three-dimensional radula (Vokes, 1971; Radwin & D'Attilio, 1976), an outermost shell layer composed of calcite (Figures 1–6), a D-shaped operculum having a lateral nucleus (Figures 7–11), separate openings for the accessory boring organ and ventral pedal gland (Carriker, 1981; Carriker & Gruber, 1999), and flask-like egg capsules with sutures in the ampulliform position (Perry & Schwengel, 1955; MacKenzie, 1961; Radwin & Chamberlin, 1973; D'Asaro, 1986, 1991; Herbert, 2002).

Phylogenetic relationships between *Eupleura* and other ocenebrine genera are poorly understood. Vermeij & Vokes (1997) divided the Ocenebrinae into two main groups based upon whether the shell's siphonal canal is sealed or open. These authors assigned *Eupleura* to the open canal ocenebrines, which also include *Crassilabrum* Jousseaume, 1880; *Forreria* Jousseaume, 1880; and *Urosalpinx* Stimpson, 1865; among others. Radular types, shell microstructure, protoconchs, early post-larval sculpture, and other features of the adult shells in this group, however, are heterogeneous (Herbert, unpublished data), and this group is very likely polyphyletic. Although *Eupleura* lacks the sealed canal condition, its species tend to have narrowly open canals that are closer to the sealed canal than the open canal condition. Other characters, including the presence of a thin rather than a thick outer layer of calcite and expanded lamellose varices, are also consistent with a closer phylogenetic relationship of *Eupleura* to the sealed canal ocenebrines, which include *Ocenebra* Leach in Gray, 1847; *Ocenebrina* Jousseaume, 1880; and *Ocenebrellus* Jousseaume, 1880.

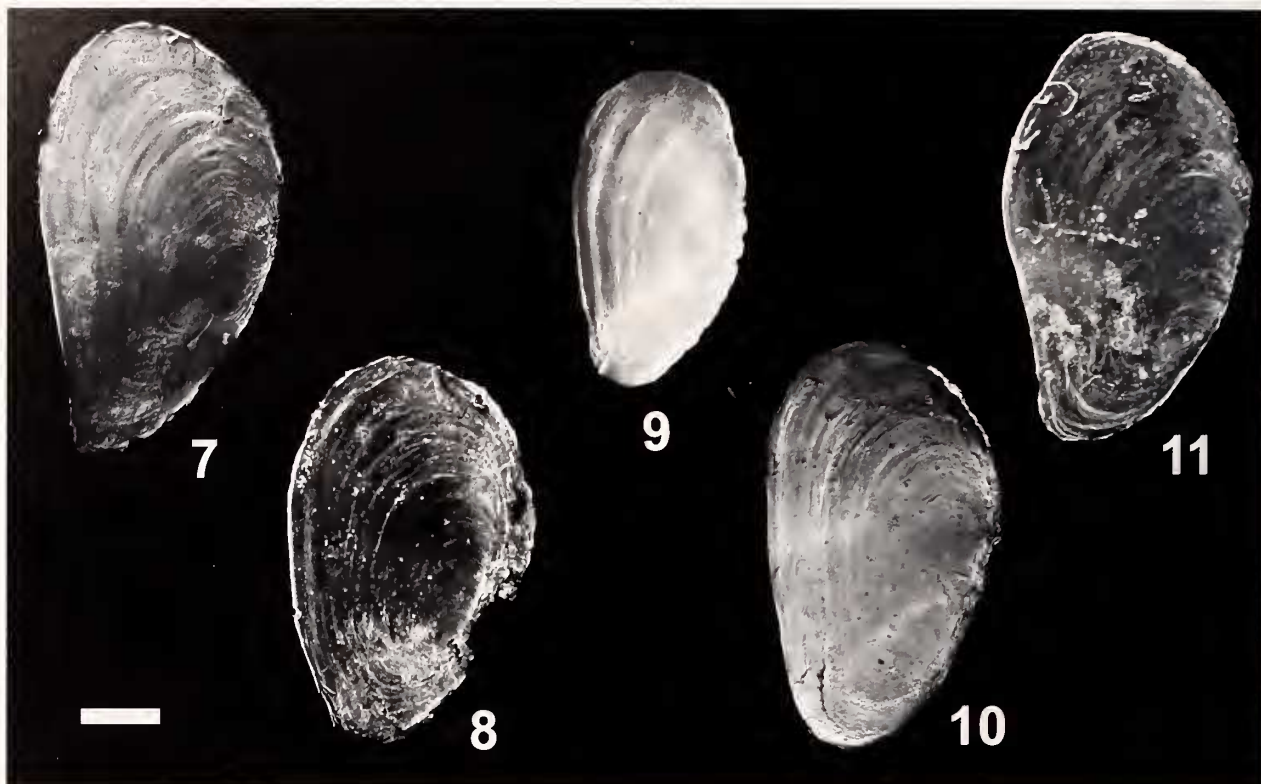
Eupleura engerrabunda Herbert, sp. nov.

(Figure 12)

Diagnosis: As for *Eupleura kugleri*, but with narrower aperture, heavier denticles, knob-like rather than cord-like



Figures 1–6. Scanning electron micrographs of fracture surfaces of shell microstructures of *Eupleura* species (all specimens are in the collection of the author). Surfaces shown are fractured parallel to growing edge with outermost portion of the shell at the top of the photos. Figure 1. *Eupleura nitida* (Broderip, 1833) (Scale bar = 100 μm). Figure 2. *Eupleura triquetra* (Reeve, 1844) (Scale bar = 1 mm). Figure 3. *Eupleura vokesorum* sp. nov. (Scale bar = 100 μm). Figure 4. Amorphous outer calcite layer of *Eupleura vokesorum* sp. nov. (Scale bar = 10 μm). Figure 5. Innermost layer of crossed-lamellar aragonite of *Eupleura vokesorum* sp. nov. (Scale bar = 10 μm). Figure 6. Middle layer of crossed-lamellar aragonite of *Eupleura vokesorum* sp. nov. (Scale bar = 10 μm).



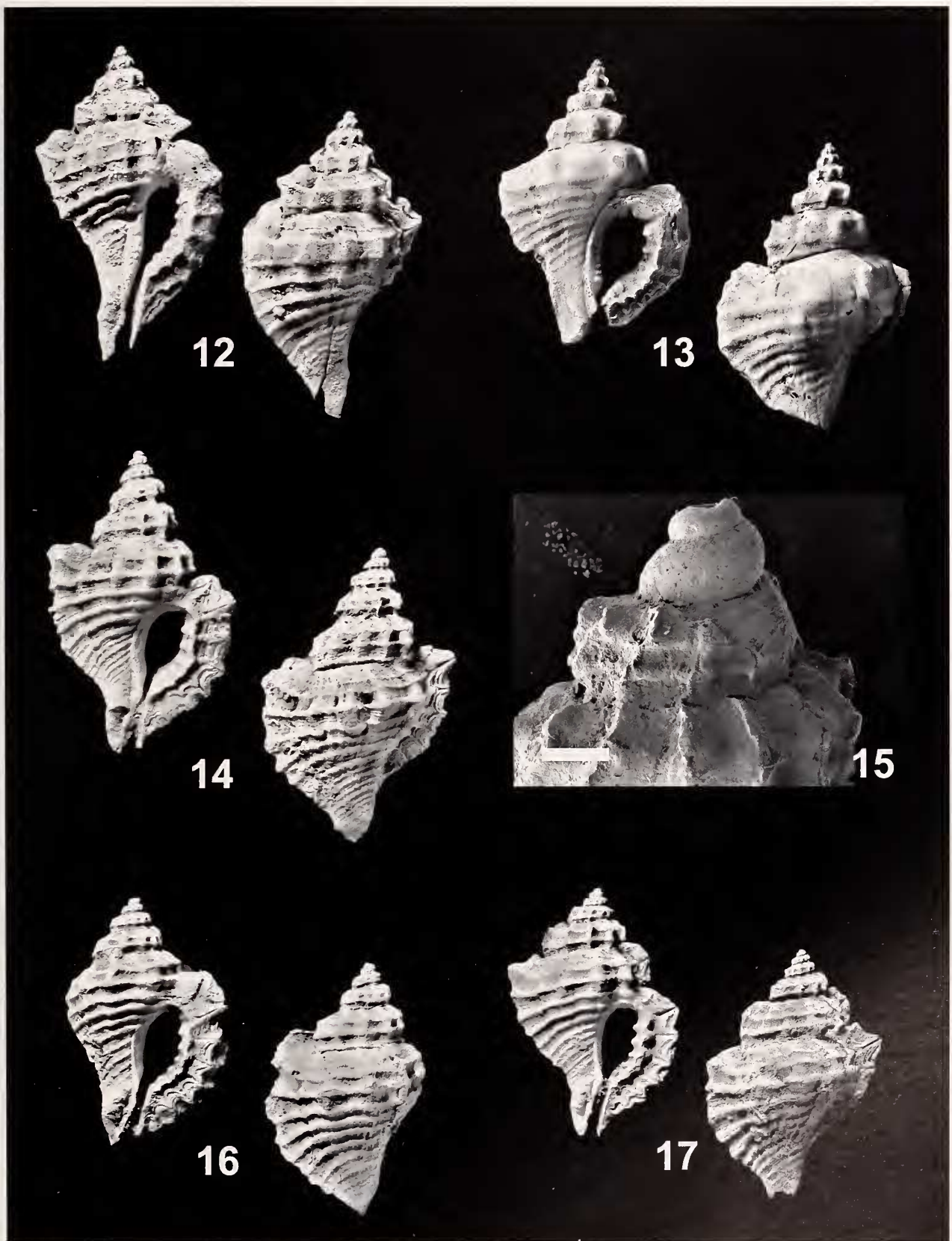
Figures 7–11. Scanning electron micrographs of opercula of *Eupleura* species (all specimens are in the collection of the author). Figure 7. *Eupleura triquetra* (Reeve, 1844). Figure 8. *Eupleura pectinata* (Hinds, 1844). Figure 9. *Eupleura nitida* (Broderip, 1833). Figure 10. *Eupleura vokesorum* sp. nov. Figure 11. *Eupleura muriciformis* (Broderip, 1833) (Scale bar = 1 mm).

parietal node, longer siphonal canal, stronger axial ribs, less-sloped sub-sutural ramp, and periphery formed by second rather than third cord anterior to suture.

Description: Shell small for genus, outline fusiform with dorso-ventrally flattened body whorls. Maximum shell height 21.5 mm. Teleoconch with at least seven whorls; protoconch unknown. Early teleoconch whorls tabulate with axial lamellae becoming sloped with axial ribs on later whorls. Later teleoconch whorls having eight strong cords; one cord above shoulder, seven on body; four to five closely spaced and less prominent cords on anterior canal. Shell surface reticulate. Shoulder cord at varix not

adapically upturned but longer than other cords at varix. Periphery formed by second cord anterior to suture on late teleoconch whorls. Axial ornamentation on early whorls consisting of ten or eleven lamellae becoming two varices with four intervarical ribs between each pair of varices by penultimate whorl. Intervarical ribs prominent, elongate on last whorl, beginning at shoulder and fading gradually into body whorl. Four varices present on shell; two varices on penultimate whorl and two varices on final whorl. Varices aligned, not offset. Varices moderately thickened, and not greatly expanded; outer margin of varices continuous. Aperture ovate, small, and heavily den-

Figures 12–17. *Eupleura* species. Figure 12. *Eupleura engerrabunda* Herbert, sp. nov. UCMP 198993 (Holotype); locality: Río Chacamax, about 5 km E of Palenque, Chiapas, Mexico; Late Miocene, Type Zuluzum (= UCMP S-245); height 21.5 mm, diameter 13.2 mm. Figure 13. *Eupleura gravidentata* Herbert, sp. nov. UCMP 198997 (Holotype); locality: Arroyo Dorrera, upstream, northwest of Usiacuri, Atlantico, Colombia; Pliocene, Lower Tubará Group (= UCMP S-7374); height 26.0 mm, diameter 17.9 mm. Figures 14–17. *Eupleura kugleri* Jung, 1965. Figure 14. USNM 519545; locality: Cantaure, Paraguaná Peninsula, Falcón, Venezuela; Early Miocene, Cantaure Formation (= USGS loc. 25271); height 21.6 mm, diameter 13.8 mm. Figure 15. USNM 519548; locality: Same locality as Figure 14; scanning electron micrograph of protoconch and early teleoconch whorls (scale bar = 200 μ m). Figure 16. USNM 519546; locality: Same locality as Figure 14; height 16.9 mm, diameter 10.8 mm. Figure 17. USNM 519547; locality: Same locality as Figure 14; height 16.0 mm, diameter 11.3 mm.



titled; six or seven strong denticles on outer lip, and one denticle at posterior portion of columellar wall. Siphonal canal of moderate length, straight, and narrowly open.

Holotype: UCMP 198993, height 21.5 mm, diameter 13.2 mm.

Type locality: "Type Zuluzum." Miocene deposits, Chiapas, Mexico, on Río Chacamax, about five km east of Palenque (UCMP loc. S-245).

Occurrence: Early Late Miocene, "type Zuluzum," Chiapas, Mexico.

Etymology: A combination of "Engerrand" (the name of the paleontologist who first published on the "Zuluzum" fauna [Engerrand and Urbina, 1910]) and *errabunda* (L.), wandering (in reference to an early, but temporary, geographic expansion of the genus *Eupleura* from the northern coast of South America into the Yucatan region).

Discussion: *Eupleura engerrabunda*, sp. nov. is superficially similar to the Early Miocene species *Eupleura kugleri* but differs in having a narrower aperture with heavier denticles, a knob-like rather than a cord-like parietal node, a longer siphonal canal, stronger axial ribs, a less-sloped subsutural ramp, and a periphery formed by the second rather than the third cord anterior to the suture.

Eupleura engerrabunda was discovered in the UCMP collections in material collected from the type locality of the "Zuluzum" fauna of southern Mexico. The original collection of Zuluzum fossils described by Engerrand & Urbina (1910) is apparently lost (M. Perrilliat, 1999, personal communication), and the UCMP collections may represent the only material available for study. In the Tulane University locality ledger, there is mention of one other collection site, TU 1201, which may refer to the "Type Zuluzum" locality. I was not able to find this material, however, during a recent visit to the Florida Museum of Natural History in Gainesville, where the Tulane collection currently resides.

In their original paper, Engerrand & Urbina (1910) suggested the Zuluzum fauna was Early Miocene in age, but subsequent workers preferred a Middle Miocene (Woodring, 1928; Perrilliat, 1963, 1974) or even "(?) Late" Miocene age (Jung, 1989) based on faunal evidence. Strontium isotopic analyses of fossil gastropod shells from the UCMP collections using the standard strontium isotopic seawater curve of Hodell & Woodruff (1994) give a conservative early Late Miocene age (10.2 to 9.4 Ma) estimate (Herbert & De La Rocha, unpublished data).

The type locality for this new species is one of the earliest documented expansions of the genus beyond the northern coast of South America. The absence of *Eupleura* species resembling *Eupleura engerrabunda* in younger deposits of eastern Mexico suggests that this initial expansion was ultimately unsuccessful.

Eupleura gravidentata Herbert, sp. nov.

(Figure 13)

Diagnosis: As for *Eupleura leonensis* Mansfield, 1930, but with more sloped body whorl, three rather than five intervarical axial elements, node-like rather than rib-like intervarical axial elements, and periphery formed by third rather than second cord anterior to suture on late teleoconch whorls.

Description: Shell of moderate size for genus, 26 mm in maximum shell height, fusiform in shape. Spire high, with about seven whorls. Protoconch missing. Axial elements lamellose on early whorls, about 11 in number. Axial elements becoming more node-like on later whorls and reduced to eight in number. On penultimate whorl, two low, blade-like varices forming at every fourth axial; on final whorl, varices thickened and expanded. Non-varical axial elements forming sub-obsolete intervarical nodes. Four varices total on shell. Shoulder of early whorls well-formed, becoming weak on penultimate whorl; shoulder on last whorl strongly sloped, with periphery formed by third cord anterior to suture. First three spire whorls high with three strong cords. Later whorls lower with weaker cords. Eight spiral cords on last whorl: uppermost three cords evenly and widely spaced; lower cords crowded. Cords weakening towards anterior canal. Canal incomplete. Aperture small, with six heavy apertural denticles on inside of outer lip, numerous fine rugae on columella, one large denticle on posterior portion of columella, and two low, closely spaced denticles situated on flattened, posterior portion of aperture.

Holotype: UCMP 198997, height 26.0 mm (incomplete), diameter 17.9 mm.

Type locality: "Arroyo Dorrera, upstream, northwest of Usiacuri, Atlántico, Colombia." Lower Tubará Group (UCMP S-7374).

Occurrence: Pliocene or earliest Pleistocene. Lower Tubará Group, Colombia.

Etymology: *graviter* (L.), heavily + *dentata* (L.), toothed (in reference to the numerous, large teeth surrounding the aperture).

Discussion: This species is superficially similar to *Eupleura leonensis* from the Pliocene of Florida in having a large shell with a high, narrow spire, thickened and expanded varices, and a heavily denticulated aperture. *Eupleura gravidentata*, sp. nov. differs, however, in having three rather than five intervarical axial elements, node-like rather than rib-like intervarical axial elements, and a periphery formed by the third rather than the second primary cord anterior to the suture on the late teleoconch whorls. *Eupleura gravidentata* is also superficially similar to the Miocene to Recent *Eupleura muriciformis* but has a taller spire, less tabulate whorls, and much

stronger and more numerous apertural denticles and columellar rugae.

Several fossil taxa (e.g., *Calophos barauoanus* Anderson, 1929; *Soleuosteira lasletti* Anderson, 1929) also collected at UCMP S-7374 with *Eupleura gravidentata* allow a tentative correlation of the type locality of this species with the lower Tubará Group, which is now considered Pliocene or even earliest Pleistocene in age (Jung, 1989; Vokes, 1990).

Eupleura kugleri Jung, 1965

(Figures 14–17)

Eupleura kugleri? JUNG, 1965, 524–525, pl. 70, figs. 3–6.

Description: “Shell of medium size. Spire high. Whorls moderately inflated, about seven in number. Protoconch and surface of first sculptured whorls not well preserved. Protoconch probably consists of about 1½ volutions. Axial sculpture formed by regularly spaced ridges in early stages, two of which are transformed on later whorls into sharp, nearly opposite varices. Between the varices there are generally three axially elongate knobs, which, however, may be absent. Early whorls sculptured [sic] by two prominent spirals, the upper one marking a shoulder. Subsequently secondary spirals are intercalated. On the body whorl the shoulder disappears. Body whorl with about seven primary spirals which form projections at the margin of the outer lip. Their interspaces are smooth or have inconspicuous minor spirals. Suture slightly appressed. Aperture oval. Outer lip with a row of six denticles at a short distance from its margin. Inner lip smooth. Siphonal canal moderately broad, slightly bent backwards, short” (Jung, 1965).

Holotype: NMB H 13715, height 24.1 mm, diameter 14.4 mm.

Type locality: Cantaure Formation, Paraguaná Peninsula, District of Falcón, Venezuela.

Occurrence: Early Miocene deposits of Venezuela and Colombia.

Discussion: *Eupleura kugleri* is the oldest known member of the genus predating first occurrences of other tropical American *Eupleura* species in the fossil record by at least ten million years and subtropical to temperate species in the western Atlantic by at least 15 million years. Surprisingly, this species is exceedingly similar to the living eastern Pacific species *Eupleura nitida* (Broderip, 1833), and it is clear that this line has evolved little in the last 20 million years (compare Figures 14, 17 with Figures 29–32). Characters that distinguish the two species are the scabrous rather than smooth shell surface, the rib-like as opposed to node-like intervarical axial elements, and the four rather than three intervarical axial elements in *E. nitida*.

In his original description, Jung (1965) estimated the number of protoconch whorls of *Eupleura kugleri* to be 1.5. Examination of well-preserved material of this species, however, indicates a protoconch with 2.5 whorls (Figure 15).

The Cantaure Formation of Venezuela from which this species was first described has been dated as late Early Miocene (Burdigalian) by Hunter & Bartok (1974). *Eupleura kugleri* is common in deposits of the Cantaure Formation (USNM 9317 and NMB collections), at locality USGS 11641 west of Sinu, Bolívar, Colombia identified as Early Miocene by Woodring (1959), and in UCMP collections recorded as the “Chicguage Formation” of Venezuela (UCMP S-8360). The type locality of the latter is equivalent to the Cantaure Formation (G. Vermeij, 2000, personal communication).

Eupleura lehneri Jung, 1969

(Figures 18–21)

Eupleura lehneri JUNG, 1969, 491–492, pl. 50, figs. 1–4.

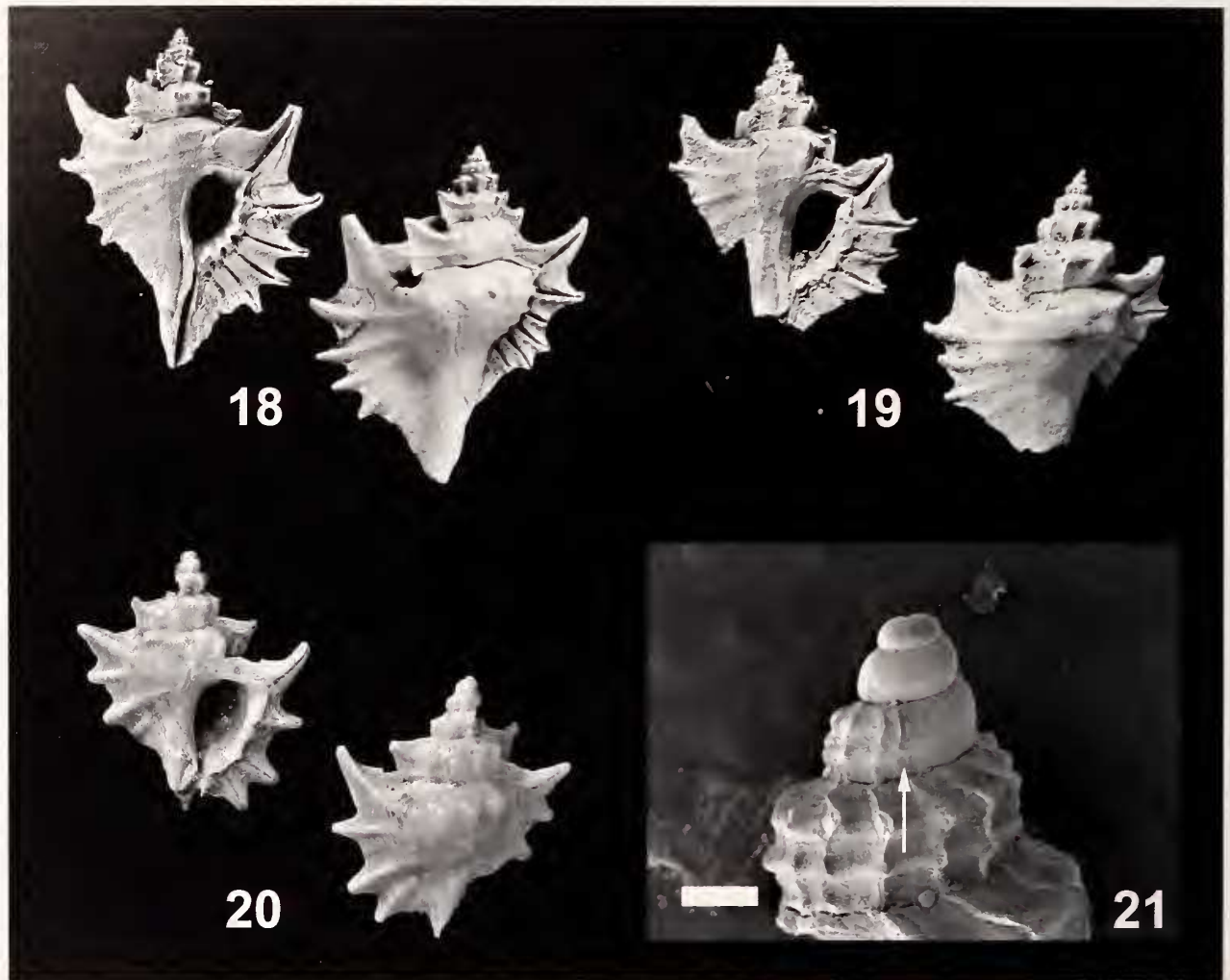
Description: “Of small to medium size. Protoconch consists of two smooth whorls; initial whorl small. Postnuclear whorls numbering up to seven. Early sculpture consists of two spirals and numerous axials (about 14 on first sculptured whorl). The upper spiral forms a prominent shoulder on the first sculptured whorl already. Number of axials decreases rapidly on later whorls, but then becomes more and more lamellar. First varix usually appears on the penultimate whorl only. Later varices are almost directly opposite the earlier ones. Intervarical axials three but reduced to broad nodes on the shoulder or even become obsolete. Body whorl moderately inflated. Last varix with six spines which are grooved anteriorly. The uppermost one is larger than the others and is pointing steeply upwards. Body whorl with spirals corresponding to the spines. Outer lip with denticles corresponding to the interspaces of the spines. Inner lip smooth. Aperture subtriangular, most acute angle pointing toward base. Siphonal canal moderately long, straight, not bent backward” (Jung, 1969).

Holotype: USNM 645346, height 27.0 mm, diameter 19.6 mm.

Type locality: Melajo Clay Member of the Springvale Formation, Trinidad.

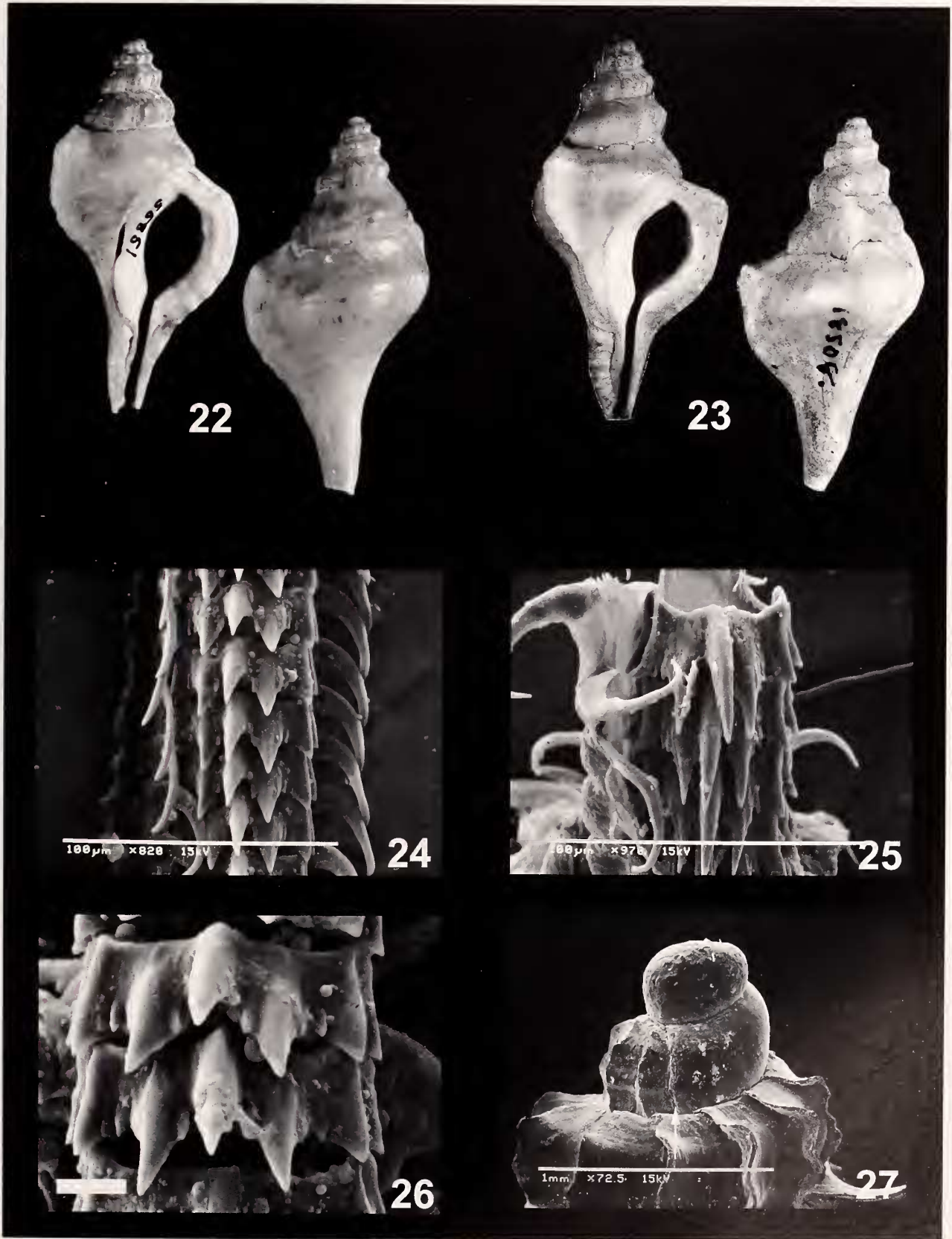
Occurrence: Early Pliocene, Springvale Formation, Trinidad; Early Pliocene, Río Banano Formation, Costa Rica (Atlantic side).

Discussion: In the collections of the NMB, there are several examples of this species from the Pliocene Río Banano Formation at Quitaría, Costa Rica (NMB loc. 18096, PPP 00679), the first for *Eupleura lehneri* outside of the type locality. The Costa Rican shells (Figure 20) differ



Figures 18–21. *Eupleura lehneri* Jung, 1969. Figure 18. USNM 645346 (Holotype); locality: Melajo River, northeastern Trinidad; Early Pliocene, Melajo Clay Member of Springvale Formation (= USGS 21178); height 27.0 mm, diameter 19.6 mm. Figure 19. USNM 519549 (Paratype); locality: Same as Fig. 18; height 20.3 mm, diameter 17.8 mm. Figure 20. NMB H 18316; locality: Quitarfa, Río Banano, Limón Province, Costa Rica; Early Pliocene, Río Banano Formation (= NMB 18096, PPP 00679); height 11.8 mm, diameter 10.2 mm. Figure 21. USNM 519550; locality: Same as Figure 18; scanning electron micrograph of protoconch and early teleoconch whorls (scale bar = 200 μ m; arrow points to protoconch/teleoconch transition).

Figures 22–27. *Eupleura limata* Dall, 1890. Figure 22. USNM 55851 (Holotype); locality: “The head of the Gulf of California, near the estuary of the Colorado River;” height 41.5 mm, diameter 18.5 mm. Figure 23. SBMNH 118508; locality: San Felipe, Baja California, Mexico; height 39.2 mm, diameter 18.5 mm. Figures 24–26. SBMNH 144608; locality: Playa Alemajas, 6 km north of San Felipe, Baja California, Mexico; scanning electron micrographs of the radula showing variation in rachidian cusp length (scale bar = 100 μ m in Figures 24, 25; scale bar = 10 μ m in Figure 26). Figure 25. USNM 61-7; locality: San Felipe, Baja California, Mexico; in 9 m. Figure 27. Scanning electron micrograph of the protoconch and early teleoconch whorls (scale bar = 1 mm; arrow points to protoconch/teleoconch transition).



somewhat from material collected at the type locality (Figures 18–19) in being much smaller (less than 10 mm), and in having fewer whorls and more prominent axial sculpture between the varices. Aperture shape, spire shape, and, particularly, the spinose varices, however, are all identical to those observed in the type material. I tentatively consider the Costa Rican material to be juvenile forms of *E. lehneri*, although additional material may eventually show that these are mature forms of a distinct species. The prominent axial nodes seen in the Costa Rican material, for example, were not observed in any ontogenetic stages of *E. lehneri* from the type locality.

Controversy surrounding the relationship between *Eupleura lehneri* and *Eupleura pectinata* is discussed below under *Eupleura thompsoni* Woodring, 1959.

Eupleura limata Dall, 1890

(Figures 22–27)

Eupleura muriciformis var. *limata* DALL, 1890a, 146.
DALL, 1891, 175.

Description: “. . . the intervarical nodes are obsolete; the whole surface nearly smooth; there are but two or three varices in all, and they are narrow and not prominent. This variety reaches a length of 40 and a diameter of 18.5 mm” (Dall, 1890a).

Revised description: Shell large for genus. Maximum height 41.5 mm. Eight teleoconch whorls in adult; protoconch of 1.5 smooth, rounded whorls. Spire high. Whorls with wide, sloped, sub-sutural ramp. Early whorls with 12–14 axial lamellae becoming more rounded on later whorls. Axial elements on last teleoconch whorl obsolete. Early spiral ornamentation consisting of two cords and third partially concealed by subsequent whorl. Spiral cords and axial nodes on last whorl obsolete or nearly so. On penultimate and final teleoconch whorl, periphery formed by third primary cord below suture. One or two varices sometimes present on penultimate whorl; two varices on final teleoconch whorl. Varices rounded, rib-like. Aperture strongly ovate, with six sub-obsolete denticles on outer lip. Siphonal canal long, straight, moderately open. Shell surface smooth, glossy. Shell color solid white with light yellow, orange, or purple tint.

Holotype: USNM 55851, height 41.5 mm, diameter 20.0 mm.

Type locality: “The head of the Gulf of California, near the estuary of the Colorado River.”

Occurrence: Recent: Northwestern Gulf of California near San Felipe, Puertocitos, and El Golfo de Santa Clara, Mexico.

Habitat: Intertidal to 15 m on mud and sand bottom.

Discussion: *Eupleura muriciformis* var. *limata* Dall,

1890, has been overlooked by many workers (e.g., Radwin and D’Attilio, 1976) or synonymized erroneously under either *Eupleura muriciformis* or *Eupleura triquetra*. The shell morphology of Dall’s variety is only generically similar to that of *E. muriciformis* but is easily confused with *E. triquetra*, which is nearly identical in shell morphology. The type specimens and additional material for all three taxa are figured herein. *Eupleura triquetra* is found throughout the Gulf of California except in the northwestern-most region near San Felipe and El Golfo de Santa Clara, where *E. limata* is restricted. *Eupleura limata* differs from *E. triquetra* in having weaker spiral cords and intervarical ribs, a less developed shoulder spine on the varix, a more expanded parietal shield, and a glossy shell surface rather than the chalky white intritcalx of *E. triquetra*. *Eupleura limata* has a white, light yellow, or light orange shell color without spiral bands; beneath its intritcalx. *E. triquetra* has a white, grey, or greyish-purple base color, often with one to three broad spiral bands of brown. Both species have paucispiral protoconchs indicative of direct development (Figures 27, 78).

Although these differences in shell morphology and color are subtle, there are striking differences in the morphology of the rachidian teeth between these forms, which support regarding *Eupleura muriciformis* var. *limata* as a full species. The rachidian of *Eupleura triquetra* differs from that of *E. limata* in having a much wider gap between the lateral and central cusps of the rachidian tooth, a longer central cusp that has a wide base, more slender lateral cusps, weaker and sometimes bifurcated intermediate denticles, and fewer and weaker marginal denticles (Figures 24–26, 75–77). The rachidian of *E. limata* further varies in the length of the central, lateral, and marginal cusps (Figures 24–25).

Cryptic speciation and a high level of endemism may be a predominant biogeographic pattern in the northern Gulf of California. Marko & Vermeij (1999) found that molecular sequence divergence in *Mexacanthina angelica* (Oldroyd, 1918) from Bahía de Los Ángeles and San Felipe was much higher than expected considering the close geographic proximity of these two localities (<100 km). San Felipe harbors other molluscan endemics as well (von Cosel, 1992; Hertz et al., 1992; Keen, 1971), possibly due to “peculiar” ecological conditions in that area, which include fine sediments and murky water (McLean, 1969:121). Because of the close proximity of the Colorado River to San Felipe, one possible scenario is that fluctuations in flow rates during the Pleistocene (Dalrymple & Hamblin, 1998; Guerro et al., 1999) have contributed to conditions favorable for the isolation and divergence of populations in the northern Gulf of California.

Humans began diverting the Colorado River, however, starting in the 1930’s, which caused a dramatic decrease in sediment and nutrient flow into the delta (Fradkin, 1996) and triggered the collapse of the delta ecosystem.

Ecosystem collapse has been particularly severe in the marine portion of the estuary (Luecke et al., 1999; Kowaleski et al., 2000), where *Eupleura limata* was previously recorded. Some mollusks endemic to the delta, such as the bivalve *Mulinia coloradoensis*, are being replaced by more fully marine species in the Gulf as marine conditions encroach further into the delta (Flessa & Téllez-Duarte, 2001).

The effects of the river diversion on populations of *E. limata* are unknown. In museum collections, no live collected material is known from the San Felipe area after the early 1970's. During a recent survey of the intertidal flats of San Felipe and El Golfo de Santa Clara, I was able to find only a few dark-stained, sub-fossil shells of *E. limata* occupied by hermit crabs but no live animals. Because *E. limata* was endemic to this area, it is possible that many or all populations of this species are now extinct. However, it does not appear to have been replaced by the more fully marine species *Eupleura triquetra*, which is abundant in other parts of the Gulf. Additional surveys are needed to assess the status of *E. limata*.

Studies of Pleistocene fossils from southern California and northern Baja California, Mexico in the LACMIP and UCMP collections indicate that the countless reports of Pleistocene fossils assigned to *Eupleura muriciformis* and *Eupleura limata* in the literature (e.g., Chace, 1956; Emerson & Chace, 1959; Kanakoff & Emerson, 1959; Emerson, 1980) are probably all references to *Eupleura triquetra*. A typical fossil specimen from the southern California area (Figure 79) has strong spiral sculpture and four strong axial nodes, which characterize *E. triquetra* rather than *E. limata*.

Eupleura muriciformis (Broderip)

(Figures 28–40)

Ranella muriciformis BRODERIP, 1833, 179. SOWERBY, G.B. JR., 1841, pl. 88, fig. 11. REEVE, 1844b, pl. 7, sp. 34. KOBELT, 1878, 129, pl. 38a, fig. 1.

Eupleura muriciformis (Broderip), TRYON, 1880, 158, pl. 39, fig. 502.

NOT:

Eupleura muriciformis (Broderip), TRYON, 1880, pl. 39, fig. 501. [= *E. pectinata*]

Eupleura muriciformis (Broderip), TRYON, 1880, pl. 39, fig. 504. [= *E. plicata*]

Eupleura muriciformis (Broderip), TRYON, 1880, pl. 39, fig. 505. [= *E. triquetra*]

Eupleura muriciformis (Broderip), DALL, 1890b, 174, pl. 5, fig. 2. SMITH, 1944, fig. 307. ABBOTT, 1974, 188, fig. 1961. KEEN, 1971, 530, no. 1024. RADWIN & D'ATTILIO, 1976, 115–116, pl. 19, fig. 5. VOKES, 1984, pl. 2, fig. 19. [= *E. vokesorum*, sp. nov.]

Description: “Ran. testá subpyriformi, fuscá, fulvá vel sordide albá, transversim striatá (striis subremotis), varicibus pinnatis, latiusculis, albidis, interstitialiter tuberculatá vel subfoliatá; columellá laevi; labri limbo intus den-

ticulato; canali elongatá, subrecurvá: long. 1½, lat. ⅞ poll” (Broderip, 1833).

Revised description: Shell large for genus with average length of 35 mm. Maximum shell height approximately 60 mm. Protoconch of 2.5 smooth rounded whorls. Spire height variable. Seven teleoconch whorls in adult specimens. Earliest whorls scalariform, with 12–14 sharp axial lamellae per whorl. Last whorl with eight or nine axial elements; two of these form blade-like varices with four (or rarely three) intervarical nodes between varices. Number of varices variable but up to seven forming per shell. Cords two or three on spire, of moderate strength, becoming six cords on major portion of body whorl, with seventh weaker cord just below suture, and numerous closely spaced cords on canal. One secondary cord occasionally present between primaries. Shoulder of spire whorls and shoulder spine on all varices formed by second cord anterior to suture; shoulder of last teleoconch whorl changing to third anterior to suture. Shoulder spine formed by thick, long, recurved and adapically extended cord. Primary cords on varix anterior to shoulder spine also sometimes forming smaller, strongly recurved spinelets. Shell surface crispate in juveniles but smooth in adults. Aperture large, round, with five or six very low denticles; columella smooth. Posterior portion of aperture flattened. Canal long, narrowly open, straight to gently recurved. Shell color dark brown, maroon, or pure white. One thin, white spiral band just below shoulder on darker shells. Thick brown band from suture to shoulder on some white shells, with a second, thinner brown band occasionally forming on canal.

Lectotype (here designated): BMNH Reg. No. 1998112 (H. Cuming Collection), height 37.1 mm, diameter 21.8 mm.

Paralectotype A: BMNH Reg. No. 1998112 (H. Cuming Collection), height 31.7 mm, diameter 19.8 mm.

Paralectotype B: BMNH Reg. No. 1998112 (H. Cuming Collection), height 59.8 mm, diameter 28.5 mm.

Type locality: Bay of Montijo, Panama, in 12 m.

Occurrence: Fossil: Late Middle Miocene, basal Caujarao Formation, Falcón, Venezuela. Early to middle Pliocene, Punta Gavilán Formation, Falcón, Venezuela. ?Pliocene, Cumana Formation, Island of Cubagua, Venezuela. Pliocene, Tubará Formation, Colombia. Late Pliocene, Canoa Formation, Manabí Province, Ecuador. Pleistocene, Lomita Marl, San Pedro, California. Recent: Guaymas, Mexico and Bahía Concepcion, Baja California, Mexico south to Peru (see discussion).

Habitat: Intertidal to 30 m on mud bottom.

Discussion: *Eupleura muriciformis* is commonly confused with *Eupleura vokesorum*, sp. nov., and the two species overlap geographically over much of their re-

spective ranges. They differ greatly, however, in both depth of habitat and shell morphology. *Eupleura muriciformis* is found primarily on mud from the intertidal zone to depths of 30 m, whereas *E. vokesorum* occurs on coarser sediments from 20 to 200 m. The Recent shells of *E. muriciformis* differ from those of *E. vokesorum* in having (usually) four rather than three intervarical nodes, a crispate rather than a smooth shell surface, more adapically directed shoulder spines, a broader aperture, a lower spire, a less sharply defined shoulder on the early teleoconch whorls, stronger spiral ornamentation in the adapical portion of the body whorl, and 12 to 14 rather than eight to ten axials on the early teleoconch whorls (Figures 28, 29, 33, 83–85, 89). Fossils of *E. muriciformis*, however, have only three intervarical nodes. *Eupleura muriciformis* also has a white shell with spiral bands of brown color, the first band covering the region between the suture and the shoulder of the body whorl and the second usually occurring at the narrow break between the main body whorl and the siphonal canal (Figure 40). *Eupleura vokesorum*, in contrast, has a solid maroon shell without any detectable banding (Figure 83). The opercula of these two species differ in the sigmoid-shaped rather than straight left edge of the operculum in *E. muriciformis* (Figures 33, 89). Their radulae are similar.

A lectotype for *Eupleura muriciformis* is designated here in order to clarify the identity of this species. The lectotype selected is one of three shells in the type lot in the BMNH. It can be distinguished from the two other syntypes (now paralectotypes A and B) in shell dimensions, which are given above, as well as in spire height and shell color. The lectotype is of average shell height for the species (~35 mm), light maroon in shell color, and has a spire roughly one third the height of the shell (Figure 28). Paralectotype A is nearly the same shell height as the lectotype, but differs in having a dark brown shell with a narrow white band, and a much lower spire (Figure 29). Paralectotype B (not figured) is an enormous specimen (nearly 60 mm in shell height), solid white in color, and has an unusually high spire. Regrettably, none of the syntypes are 'typical' for the species in shape, color, and/or size. The most common form for this species has a white shell with a thick brown band above the shoulder and a narrow band midway between the shoulder and the tip of the canal, V-shaped varices with a sin-

gle upturned spine at the shoulder, and a relatively low spire (Figure 40).

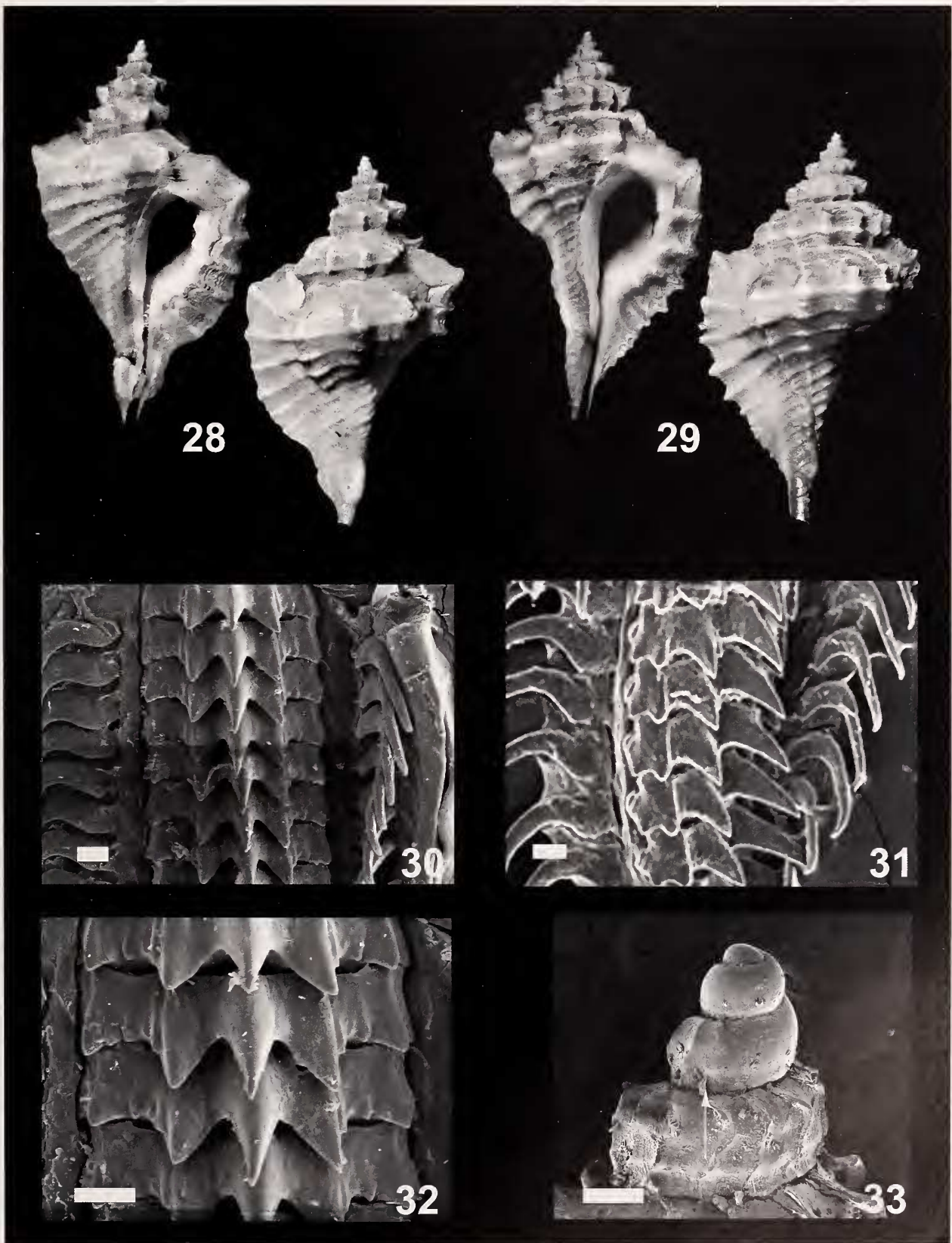
Previously, this species was reported from the Pleistocene fossil record of southern California and Baja California, Mexico and the Pliocene record of Ecuador. Pleistocene fossils in the literature recorded as *Eupleura muriciformis*, however, are all examples of *Eupleura triquetra* (see discussion under *Eupleura limata*). Pliocene fossils from Ecuador identified as *E. muriciformis* by Vokes (1989a) are probably *Eupleura vokesorum*, sp. nov. based on her concept of *E. muriciformis* as illustrated in Vokes (1984) and in her private collection now housed at the SBMNH. Unfortunately, the exact identity of the Ecuador fossils could not be confirmed as this material has been misplaced (E. Benamy [ANSP] 1998, personal communication). It is unlikely, then, that any of the fossil occurrences of *E. muriciformis* referenced in the literature refer to this species.

The additional data supplied by newly discovered fossil examples of *Eupleura muriciformis* in the paleontological collections of the LACMIP, NMB, UCMP, and USNM are significant for several reasons. First, *E. muriciformis* is one of the geologically oldest of the living species in the genus as evidenced by its occurrence in the late Middle Miocene Caujarao Formation of Falcón, Venezuela (Figure 34). Because previously reported fossils for this species were incorrectly identified, this is equivalent to roughly a 10–14 million year stratigraphic range extension.

Second, the stratigraphic and geographic occurrences of the newly discovered *E. muriciformis* fossils indicate that this species inhabited the western Atlantic for a considerable amount of time, perhaps seven million years or more, before arriving in the eastern Pacific in the Late Pliocene. There are numerous Late Miocene deposits on the eastern Pacific side of tropical America containing a range of environments (J. Todd, 2002, personal communication) and several species of *Eupleura*, but not *E. muriciformis*. Third, the present distribution of *E. muriciformis* in the eastern Pacific is relictual, since during the Late Pliocene, this species was present in both the eastern Pacific and the western Atlantic but today survives only in the eastern Pacific. Finally, the oldest fossil examples of this species have shells with three intervarical ribs, whereas most of the modern specimens have four. Other

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Figures 28–33. *Eupleura muriciformis* (Broderip, 1833). Figure 28. BMNH Reg. No. 1998112/1 (Lectotype); locality: Bay of Montijo, west coast of Panama, in 12 m; height 37.1 mm, diameter 21.8 mm. Figure 29. BMNH Reg. No. 1998112/2 (Paralectotype A); locality: Same as Figure 28; height 31.7 mm, diameter 19.8 mm. Figures 30–32. BMNH Reg. No. 1998112/1 (Lectotype), locality: same as Figure 28, scanning electron micrographs of the lectotype radula (scale bar = 10 μ m). Figure 33. LACM 37-124; locality: "Sonora, Mexico;" scanning electron micrograph of the prototconch and early teleoconch whorls (scale bar = 200 μ m; arrow points to protoconch/teleoconch transition).



species, such as *Eupleura nitida* and *Eupleura plicata*, also have four or five intervarical ribs, but the fossils of *E. muriciformis* demonstrate that this shared condition was derived independently in *E. muriciformis*.

The geographic range of modern *Eupleura muriciformis* is unclear, since many literature records of this species refer, entirely or in part, to *Eupleura vokesorum*, sp. nov. (e.g., Peña, 1970; Keen, 1971; Abbott, 1974; Radwin and D'Attilio, 1976). I have examined museum specimens from as far north as Guaymas in the Gulf of California and as far south as Tumbes, Peru in the South Pacific. Peña (1970) extended this range to Máncora, Peru, although this could refer to either *E. muriciformis* or *E. vokesorum*, which also extends into Peru. Tryon (1880) reported the occurrence of living *E. muriciformis* in the western Atlantic near Cedar Key, Florida as determined by W.W. Calkins and from labelled specimens in the Swift collection (ANSP 36513). This material has been re-identified as *Eupleura sulcidentata* Dall, 1890 (G. Rosenberg, 1998, personal communication), a superficially similar species that had not yet been described in 1880 when Tryon published his paper.

Lowe (1935) reported *Eupleura muriciformis* feeding on *Cerithium* sp. on reefs, but it is unclear whether he was referring to *E. muriciformis*, *Eupleura triquetra*, or *Eupleura vokesorum*, sp. nov. Hemingway (1975) also discussed the feeding habits of *E. muriciformis* and figured its radula, although the radula appears to be that of *E. triquetra*.

Eupleura nitida (Broderip, 1833)

(Figures 41–50)

Ranella nitida BRODERIP, 1833, 179. SOWERBY, G.B. JR., 1841, pl. 84, fig. 4. KIENER, 1843, 9, pl. 2, fig. 2; DESHAYES, 1843, 557, no. 25. REEVE, 1844b, pl. 8, sp. 45. ADAMS, 1852, 120.

Eupleura nitida (Broderip), TRYON, 1880, pl. 39, fig. 500; PERRY, 1940, 142–143, pl. 31, fig. 216; M. SMITH, 1944, 25, fig. 305. PERRY & SCHWENGEL, 1955, pl. 31, fig. 216, p. 154. KEEN, 1971, 530, no. 1025; ABBOTT, 1974, 188, no. 1962. RADWIN & D'ATTILIO, 1976, 116, pl. 19, fig. 6; VOKES, 1989b, Tulane pl. 1, figs. 5a–5b.

Description: "Ran. testá subrhomboided, valdè depressá, transversim tuberculato-striatá, (tuberculis subacutis), nigro-purpureo, interdum albo fasciatá, varicibus latis, pinnatus, lacinatis, albis; columellá laevis; labri limbo intus denticulato; canali subelongata: long. 1, lat. $\frac{5}{8}$ poll" (Broderip, 1832).

Revised description: Shell fusiform, small for genus, with maximum height around 25 mm. Protoconch with 2.5 smooth, rounded whorls. Transition into strongly ornamented early teleoconch whorls smooth. Earliest teleoconch whorls wide, tabulate, with two thick spiral cords and approximately 14 axial lamellae. Body whorl dorso-ventrally flattened. Seven teleoconch whorls in mature specimens. Axial elements reduced to ten per whorl on later teleoconch whorls, with every fifth axial element forming an expanded varix beginning on fifth whorl. Interspiral axial elements elongate, rib-like, forming raised nodules at intersection with spiral cords. Five major cords on body whorl, two or three weaker primary cords on canal, and one strong secondary cord between suture and first primary cord. Periphery of whorl formed by third primary cord below suture. Up to seven secondary cords intercalated between primaries. Shell surface with numerous calcitic microlamellae; on cords, microlamellae become vaulted scales. Shell color brown with white bands, but usually obscured by microlamellae. Aperture small, ovate. Six low denticles on inside of outer lip; single, low cord situated at posterior end of columella. Columella smooth. Siphonal canal short, narrowly open, bent to the left, weakly recurved.

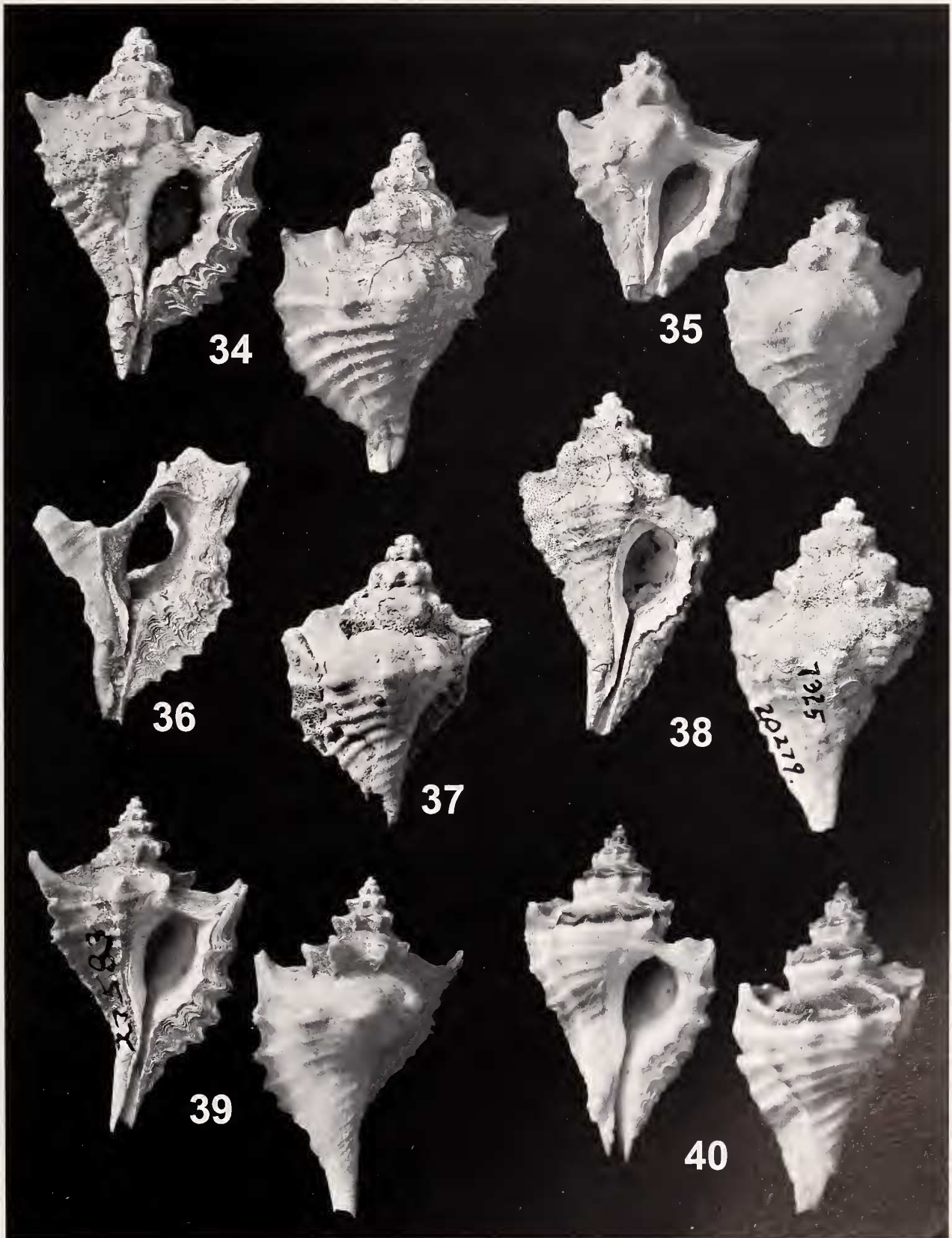
Syntypes: BMNH Reg. No. 1966648/1 (H. Cuming Collection), height 26.6 mm, diameter 20.0 mm (= Syntype 1); BMNH Reg. No. 1966648/2 (H. Cuming Collection), height 26.2 mm, diameter 14.5 mm (= Syntype 2); BMNH Reg. No. 1966648/3 (H. Cuming Collection), height 26.0 mm, diameter 16.5 mm (= Syntype 3).

Type locality: "Collumbium Occidentalem (Bay of Caracas), found under stones in the bay" (= Bahía de Caraquez, Manabí Province, Ecuador; see Jung, 1989:247).

Occurrence: Fossil: Early to middle Pliocene, Mare Formation, Cabo Blanco, Venezuela. Early to middle Pleis-

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Figures 34–40. *Eupleura muriciformis* (Broderip, 1833). Figure 34. NMB H 18310; locality: 3.5 km SSW of Pueblo Cumarebo, outcrop among houses 100 m S of road at W end of San Rafael, Falcón, Venezuela; late Middle Miocene, basal Caujarao Formation (= NMB loc. 17529); height 28.4 mm, diameter 19.2 mm. Figure 35. NMB H 18311; locality: 10 km SSE of San Lorenzo, Manabí Province, Ecuador; Late Pliocene, Canoa Formation (= NMB loc. 19142, PPP 03514); height 21.9 mm, diameter 16.7 mm. Figure 36. NMB H 18312; locality: Punta Gavilán, Falcón, Venezuela; Early to middle Pliocene, Punta Gavilán Formation (= NMB loc. 17531); height 23.7 mm, diameter 17.6 mm (incomplete). Figure 37. UCMP 198995; locality: Colombia; Pliocene, Tubará Formation (= UCMP loc. 19158); height 26.7 mm, diameter: 20.2 mm. Figure 38. LACMIP 7164; locality: Hilltop quarry, 2.5 km NW of San Pedro, California; Pleistocene, Lomita Marl; height 28.9 mm, diameter, 17.8 mm. Figure 39. CAS 116077; locality: 13 km off Sinaloa, Mexico. 18 to 31 m depth; height 27.6 mm, diameter 17.6 mm. Figure 40. CAS 116074; locality: San Blas, Mexico (Pacific); height 31.3 mm, diameter 17.8 mm.



tocene, Armuelles Formation, Río Corredor, Costa Rica (Pacific side). Recent: Mazatlán, Mexico to Chimbote, Peru (Peña, 1970).

Habitat: Intertidal to 28 m on and under stones and rocks.

Discussion: Museum labels examined from several hundred lots of *Eupleura nitida* from the museum collections listed above and habitat information collected by Spight (1983) indicate that this species lives intertidally on and under stones and rocks to 28 m in the eastern Pacific from Mazatlán, Mexico, to Chimbote, Peru. The deeper records were all recorded from Panama. A single specimen was cited by Perry (1940) as having been dredged live in 11 m off Redfish Pass, Lee County, Florida. The figured specimen was correctly identified, although the accuracy of the locality data is doubtful as no other specimens have ever been collected from this heavily sampled area.

Nevertheless, in the collections of the NMB there is one western Atlantic fossil specimen of *Eupleura nitida* from the type locality of the Mare Formation of Venezuela (NMB loc. 17512) (Figure 47). Two additional fossil examples of *E. nitida* also in the Basel collections indicate that this species was present on the Pacific coast of Costa Rica by at least the Pleistocene (Figures 48–49). In general, the fossils tend to have less expanded varices than Recent specimens, but it is difficult to determine with this limited amount of fossil material whether the shells are just immature or worn or whether there are real differences in growth patterns between them. Both fossil and Recent shells have the scabrous surface sculpture that is characteristic of this species (Figure 50).

Although the shell microstructure of this species is somewhat different than that of other species of *Eupleura* in lacking a well-defined outer calcite layer (Figure 1), the scabrous lamellae are composed of translucent calcite giving the shell a "frosted" appearance. These lamellae, therefore, may be the remnants of this outer calcite layer.

In the type lot of *Eupleura nitida* in the BMNH, there are three syntypes, one of which (Syntype 1) appears to be the shell figured by Reeve (1844b) and Tryon (1880) based on the appearance of the outer lip, which is complete in Syntypes 2 and 3 but only partially complete in Syntype 1 (Figure 41). Because there is no taxonomic confusion regarding the identity of this species, designation of a lectotype is unnecessary.

The type locality for *Eupleura nitida* is stated as "Col-

umbium Occidentalem (Bay of Caraccas), found under stones in the bay," although I was not able to locate this locality on any available maps. Jung (1989:247) noted that this could be a reference to Bahía de Caraquez, in the Manabí Province of Ecuador.

Eupleura olssoni Vokes, 1989

(Figure 51)

Eupleura thompsoni Woodring subspecies, OLSSON, 1964, 139, pl. 29, fig. 9.

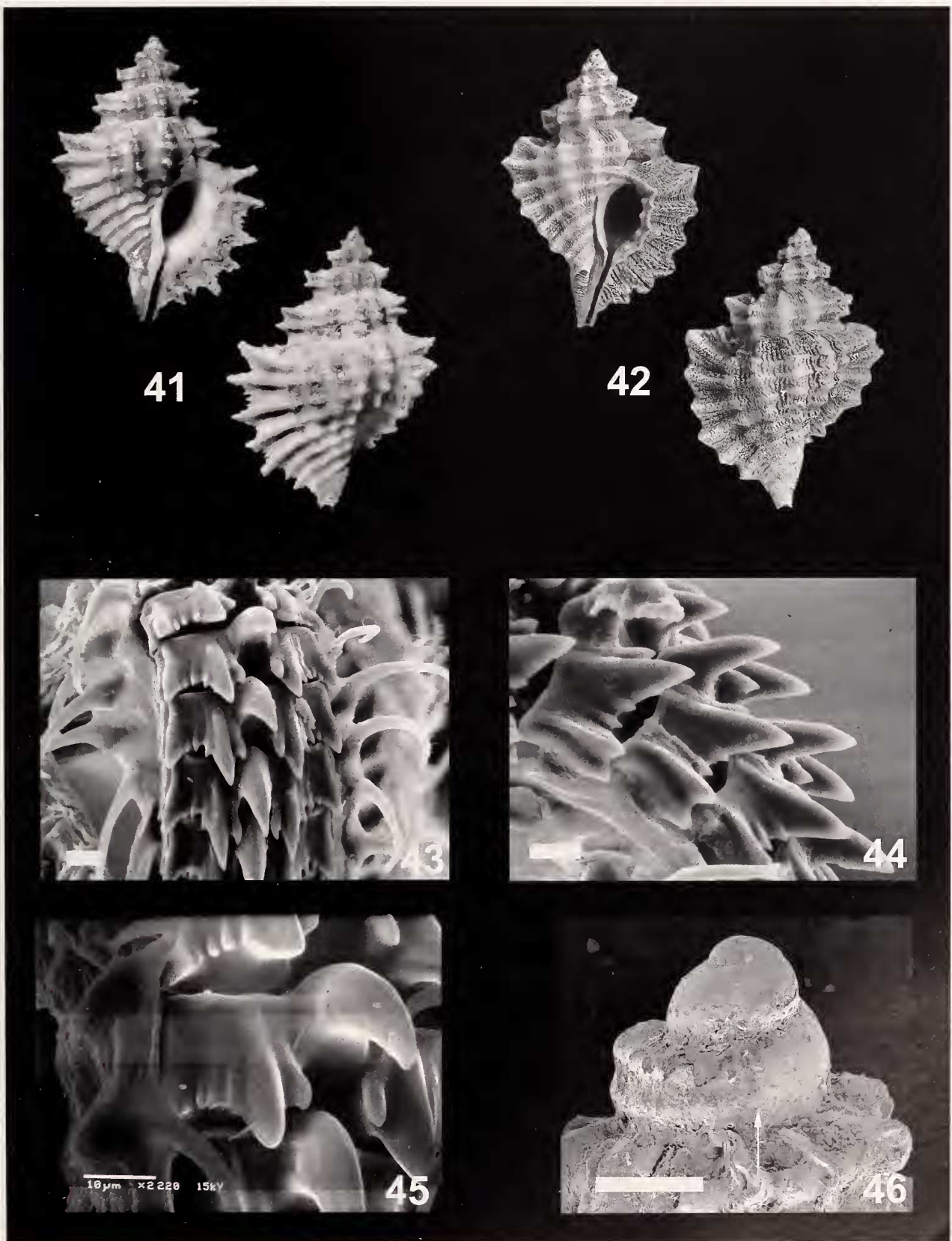
Eupleura olssoni VOKES, 1989a, 114–116, pl. 1, figs. 6–7.

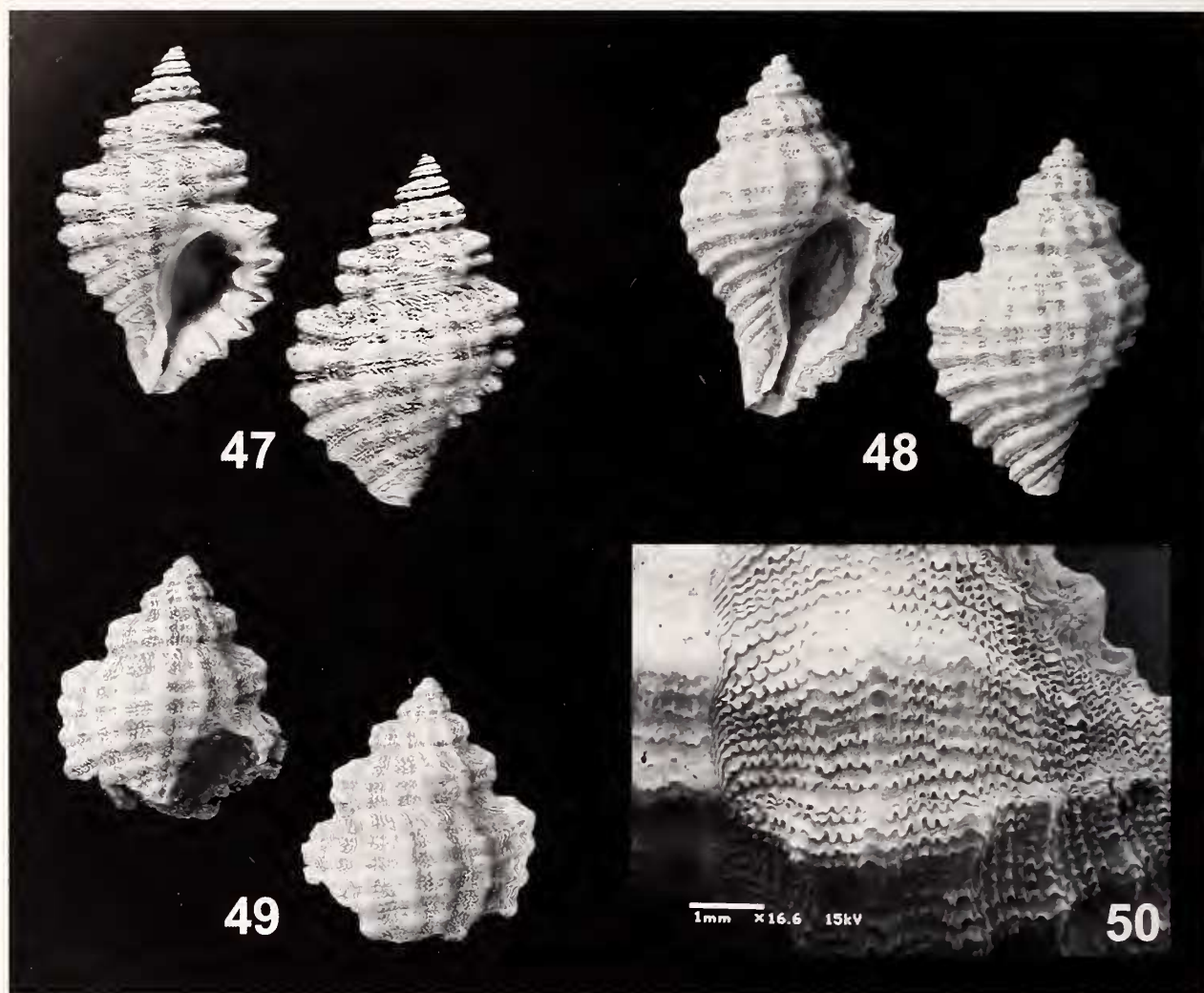
Description: "Shell small, seven teleoconch whorls; protoconch unknown. Spiral ornamentation on earliest teleoconch whorls of two sharp cords set very near anterior suture, leaving a wide, smooth, sloping shoulder ramp. On body whorl about 12 cords, one at shoulder, one weaker on the shoulder ramp, and approximately ten weaker ones anterior to shoulder, becoming progressively less strong anteriorly, very faint on siphonal canal; between each pair of major cords three to five extremely faint threads. Axial ornamentation on earliest teleoconch whorls of about 12 small lamellae, gradually reducing in number until on approximately the fifth teleoconch whorl only eight in number, with every fourth one becoming an expanded varix; three nodes remaining between each pair of varices. Varices aligned on opposite sides of the shell, with the varices of each successive whorl slightly in advance of varices on previous whorl, leaving a visible offset with varices not fused together. Intervarical nodes persisting as rounded knobs, over which the spiral ornamentation is diminished so that the knobs appear relatively smooth. Varices extended as a series of webbed scallops between points formed by extensions of the spiral cords, that at the shoulder the longest and adapically directed; on varical faces spiral cords expressed as grooves into which the shell laminae are enfolded. Aperture elongate-oval; inner lip appressed to columellar wall, with a few faint rugae reflecting underlying spiral cords. Margin of outer lip folded into the grooves of the varical face, especially at the shoulder; six strong denticles developed on inner side of outer lip, positioned between the grooves. Siphonal canal moderately long, straight, almost closed but open by a narrow slit" (Vokes, 1989a).

Holotype: USNM 445402, height 26.3 mm, diameter 17.2 mm.

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Figures 41–46. *Eupleura nitida* (Broderip, 1833). Figure 41. BMNH 1966648/1 (Syntype 1); locality: "Columbium Occidentalem (Bay of Caraccas), found under stones in bay;" height 26.6 mm, diameter 20.0 mm. Figure 42. USNM 860472; locality: Venado Beach, Panama (= TU R-188); height 26.5 mm, diameter 15.5 mm. Figures 43–45. Herbert collection; locality: Same as Figure 42; scanning electron micrographs of the radula (scale bar = 10 μ m in Figures 43–45). Figure 46. Herbert collection; locality: Same as Figure 42; scanning electron micrograph of the protoconch and early teleoconch whorls (scale bar = 200 μ m; arrow points to protoconch/teleoconch transition).





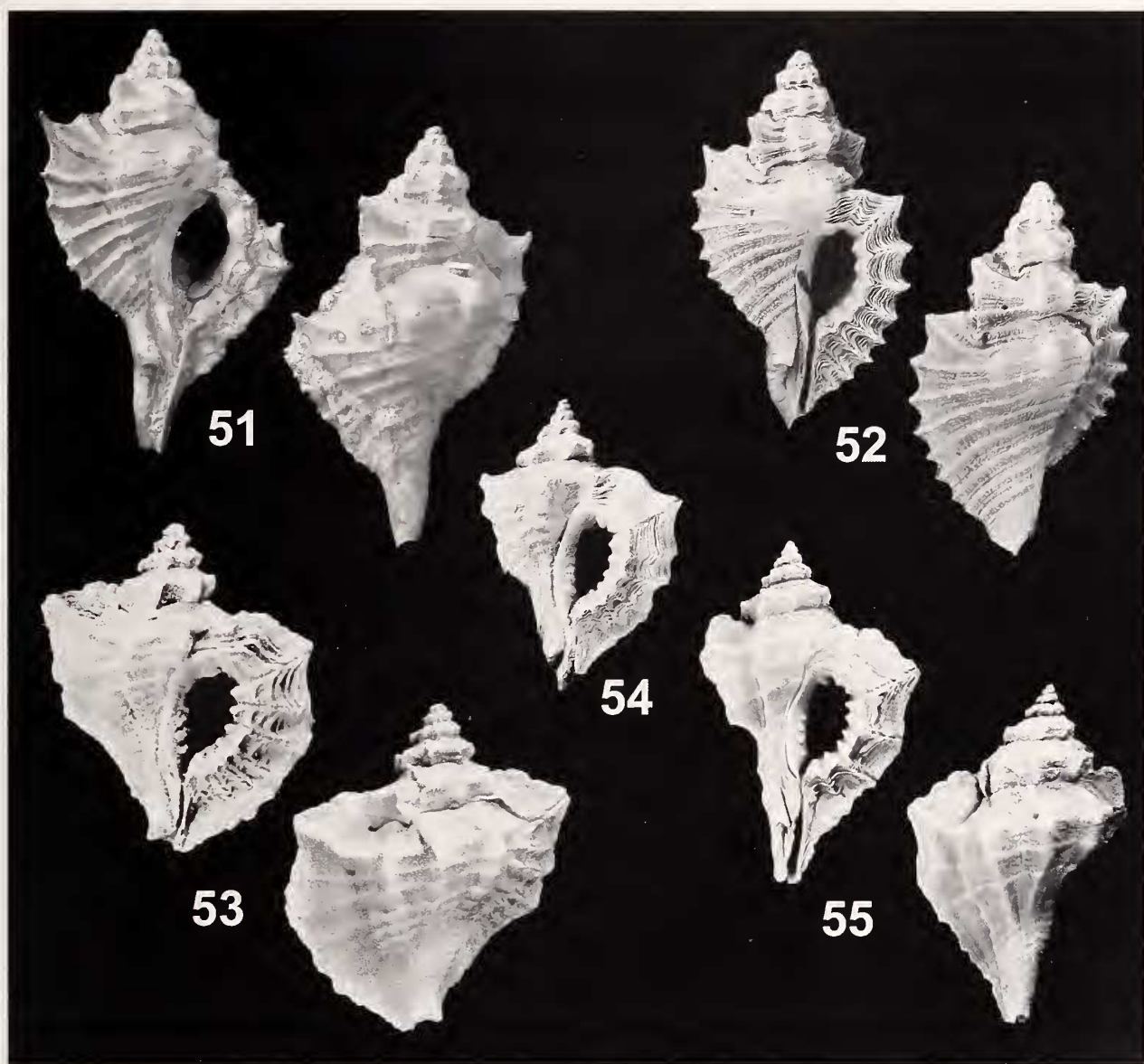
Figures 47–50. *Eupleura nitida* (Broderip, 1833). Figure 47. NMB 17512; locality: Quebrada Mare Abajo, Cabo Blanco, Venezuela; Early to middle Pliocene, Mare Formation; height 24.3 mm, diameter 16.7 mm. Figure 48. NMB H 18313; locality: Río Corredor, above bridge of Carretera Interamericana, on right bank of river, Neily, Costa Rica (Pacific); Early to middle Pleistocene, Armuelles Formation (= NMB loc. 18301, PPP 01024); height 19.3 mm, diameter 12.1 mm. Figure 49. NMB H 18314; locality: Left bank of Río Corredor, about 250 m N of bridge of Carretera Interamericana, Neily, Costa Rica (Pacific); Pleistocene? (= NMB loc. 18166, PPP 00818–00820); height 14.5 mm, diameter 12.6 mm (incomplete). Figure 50. Herbert collection; locality: Same as Figure 42; scanning electron micrograph of scabrous shell sculpture over body whorl (scale bar = 1 mm).

Type locality: Angostura Formation; Punte Verde, large point just east of Río Verde, or about 30 km east of Río Esmeraldas, Province of Esmeraldas, Ecuador (= TU 1507).

Occurrence: Late Miocene, Angostura Formation, Ecuador.

Discussion: Vokes (1989a) previously considered *Eupleura olssoni* Vokes, 1989, of the Angostura Formation of Ecuador and *Eupleura prenitida* Vokes, 1989, of the Gatun Formation of Panama to form an ancestor-descendent pair with only small differences in shell surface sculpture and shoulder spine angle between the two. More recent stratigraphic work, however, indicates that these

species were possibly contemporaries of one another. Although the Angostura Formation of northwestern Ecuador in which *E. olssoni* occurs does not contain any diagnostic planktonic foraminifera, exposed sections along the coast east of Río Verde show that the Angostura Formation overlies the Viche Formation and underlies the Onzole Formation (Vokes, 1989a). The Onzole and the Viche formations have been dated as having N12 and N16 planktonic foraminiferal faunas, respectively (Whittaker, 1988). The Angostura Formation, therefore, overlaps in age with the Late Miocene Gatun Formation of Panama, which Collins, Budd, & Coates (1996) identified as having an N14–N17 fauna.



Figures 51–55. *Eupleura* species. Figure 51. *Eupleura olssoni* Vokes, 1989. USNM 643957 (Paratype B); locality: Telembi, Río Cayapas, Ecuador; Late Miocene, Angostura Formation; height 27.6 mm, diameter 18.2 mm. Figure 52. *Eupleura prenitida* Vokes, 1989. USNM 445390 (Holotype); locality: hill-slope on east side of road from Boyd-Roosevelt Highway to Refinería Panama, S. A., about 0.5 km north of junction, just east of Cativá, Prov. of Colón, Panama; Late Miocene, Gatun Formation (= TU 958); height 31.1 mm, diameter 17.7 mm (Photographs courtesy of Emily Vokes). Figures 53–55. *Eupleura paroudia* Herbert, sp. nov. Figure 53. UF 91974 (Holotype); locality: Roadcut, pipeline cut, and quarry on Mexico Highway 180, 23 km east of junction with side road into Coatzacoalcos, Veracruz, Mexico; Early to middle Pliocene, Agueguexquite Formation (= TU 638); height 19.7 mm, diameter 16.3 mm. Figure 54. UCMP 198994 (Paratype B); locality: Same as Figure 53; height 18.0 mm, diameter 14.2 mm. Figure 55. UF 91972 (Paratype A); locality: Same as Figure 53; height 21.5 mm, diameter 14.0 mm.

Eupleura olssoni also superficially resembles the Early Pliocene to Recent *Eupleura vokesorum*, sp. nov. in having long spines extending past the margin of the varices and recurving abaperturally, a longer spine on the shoulder of the whorl than elsewhere, web-like varices, and a long narrow siphonal canal. They differ pri-

marily in the stronger spiral sculpture on the adapical portion of the body whorl and the lack of open spines on the spire whorl intervarical axials in *E. olssoni*. Vokes' (1989a) references to *Eupleura muriciformis* in her comparison of *E. olssoni* and *E. muriciformis* refer to *E. vokesorum*.

Eupleura paroudia Herbert, sp. nov.

(Figures 53–55)

Diagnosis: *Eupleura* with elongate axial ribs on body whorl, sloped body whorl, heavily denticulated aperture, broadly expanded varices, and paucispiral rather than multispiral protoconch.

Description: Shell small for genus and almost biconical in shape. Maximum height 24 mm but averaging around 20 mm. Teleoconch with seven to eight whorls; protoconch of 1.5 smooth, rounded whorls. Spire tall, scalariform; sub-sutural shelf sloping sharply from suture to shoulder. First teleoconch whorl convex; subsequent early whorls having one cord forming well-defined shoulder. Later teleoconch whorls having nine to 13 cords of moderate strength; one cord above shoulder, four to seven on body, and four to five on anterior canal. Periphery of body whorl formed by second cord anterior to suture. Shoulder cord at varix upturned and longer than rest. Axial ornamentation on early whorls consisting of ten or eleven lamellae becoming six to eight axial elements by penultimate whorl. Ribs large, elongate, beginning at shoulder but fading rapidly into body whorl. Three or four ribs between varices. Three varices present on shell; first varix on penultimate whorl and two varices on final whorl. Second varix shared by varices on penultimate and final whorls and aligned 180° apart from both. Varices bladellike, greatly expanded in mature individuals, extending from high above shoulder of last whorl to tip of siphonal canal; varices serrated at margin by ray-like projections of spiral cords. Aperture ovate, small, and heavily denticled; six or seven strong denticles on outer lip, two strong denticles across top of aperture, five to seven irregularly spaced rugae on inside lip, and one strong denticle each at both anterior and posterior portions of columellar wall. Margin of inner lip well-defined, projected away from body whorl slightly. Siphonal canal of moderate length, straight, and narrowly open.

Holotype: UF 91974, height 19.7 mm, diameter 16.3 mm.

Paratype A: UF 91971, height 21.5 mm, diameter 14.0 mm.

Paratype B: UCMP 198994, height 18.0 mm, diameter, 14.2 mm.

Type locality: Agueguexquite Formation, roadcut, pipeline cut, and quarry on Mexico Highway 180, 23 km east of junction with side road into Coatzacoalcos, Veracruz, Mexico (= TU 638).

Occurrence: Early to middle Pliocene, Agueguexquite Formation, Veracruz, Mexico.

Etymology: *paroudia* (G.), a lepidopteran (in reference to shape of the shell outline of the holotype).

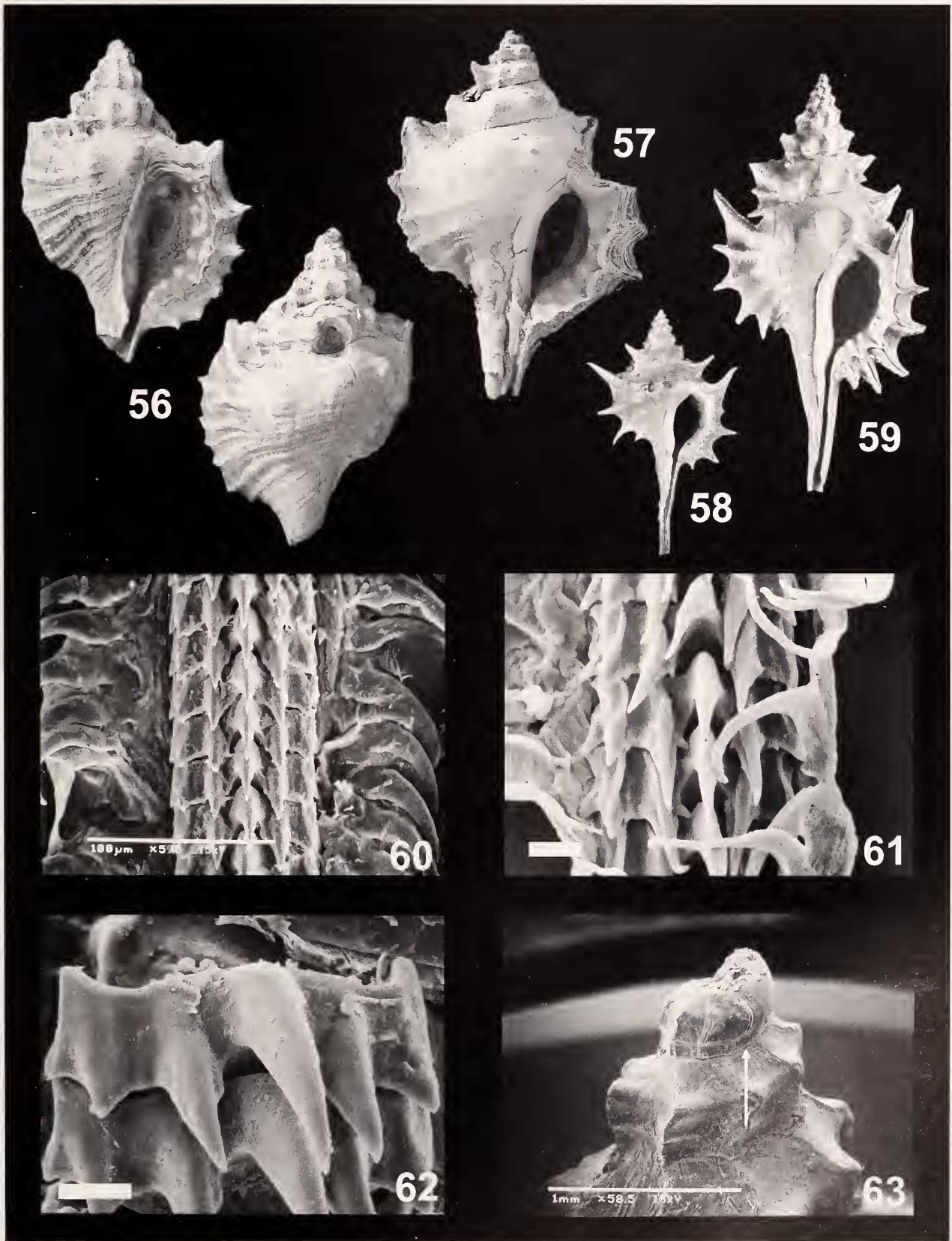
Discussion: *Eupleura paroudia*, sp. nov. was collected and first recognized as a distinct species by Emily Vokes of Tulane University but was never described. The species name designated herein was suggested by Vokes for the distinctive "butterfly shape" of the expanded varices exhibited in the holotype (Figure 53). *Eupleura paroudia* is only the second species of *Eupleura* to be reported from the fossil record of the western Gulf of Mexico; however, it does not appear to be closely related to the older, western Gulf species *Eupleura engerrabunda*, sp. nov. There are no species of *Eupleura* living in the western Gulf of Mexico today.

This new species is most similar to *Eupleura muriciformis* in shell outline but differs in having stronger and more elongate axial ribs on the body whorl, a more heavily denticulated aperture, weaker spiral ornamentation, fewer varices, a more narrowly open siphonal canal, and a paucispiral rather than a multispiral protoconch. *Eupleura paroudia* also resembles *Eupleura gravidentata*, sp. nov. from the Pliocene of Colombia in having columellar rugae and only three varices but differs in having the periphery of the whorl formed by the first rather than the second primary cord below the suture on the later teleoconch whorls, more expanded varices, and a lower spire.

The Agueguexquite Formation of Veracruz, Mexico

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Figures 56–63. *Eupleura pectinata* (Hinds, 1844). Figure 56. NMB H 18315; locality: Río Corredor, above bridge of Carretera Interamericana, on right bank of river, Neily, Costa Rica (Pacific); Early to middle Pleistocene, Armuelles Formation (= NMB loc. 18301, PPP 01024); height 29.8 mm, diameter 21.8 mm. Figure 57. UCMP 198991; locality: Arroyo Grande at Usiacuri, Dept. Atlantico, Colombia; undifferentiated Miocene (= UCMP loc. S-7607); height 41.1 mm, diameter 28.2 mm. Figure 58. CAS 113080; locality: 24 m, dredged 11.5 km west of Champerico, Guatemala; height 29.5 mm, diameter 17.0 mm. Figure 59. UF 291364; locality: Off Canal de Atuera Island, Golfo de Chiriqui, Panama; in mud and sand at 74 m; height 37.0 mm, diameter 20.0 mm. Figures 60–62. SBMNH 144604; locality: Chiriqui, Panama, in 135–185 m; scanning electron micrographs of the radula (Figure 61 shows a closeup of the nascent, partially mineralized region of the radula; scale bar = 100 µm in Fig. 60; scale bar = 10 µm in Figures 61, 62). Figure 63. CAS 113080; locality: dredged, 11.5 km west of Champerico, Guatemala, in 24 m; scanning electron micrograph of the early teleoconch whorls (scale bar = 1 mm; arrow points to protoconch/teleoconch transition).



(TU 638), in which this species is found, has been dated as Early to middle Pliocene (Vokes, 1990).

Eupleura pectinata (Hinds, 1844)

(Figures 56–63)

Ranella pectinata HINDS, 1844, 13, pl. 4, figs. 17, 18.
REEVE, 1844b, pl. 7, sp. 35.

Eupleura muriciformis (Broderip), TRYON, 1880, fig. 501.

Eupleura pectinata (Hinds), KEEN, 1971, 530, no. 1926.

ABBOTT, 1974, 188, no. 1963. RADWIN & D'ATTILIO, 1976, 116–117, pl. 19, fig. 7.

Description: “Testá fusiform, politá, cinereá; varicibus obliquis, spinis acutis muricatus; anfractibus lineis transversis elevatis instructis, inter varices tri-vel quadrifariam tuberculatis; aperturá ovali; albidá; labro intus obsolete denticulato; labio interno laevi, producto; canali elongato, recto” (Hinds, 1844).

Revised description: Shell large for genus; maximum shell height nearly 60 mm. Spire high with nine or ten whorls. Protoconch unknown. Early teleoconch whorls with sloped, but sharply defined shoulder and eight to ten axial lamellae. Later teleoconch whorls node-like with strongly sloped shoulder. Periphery formed by third cord anterior to suture. Varices aligned, two per whorl, beginning on fifth or sixth teleoconch whorl. Up to ten varices per shell. Three weak cords visible on spire whorls becoming seven cords on last whorl. Five weaker cords present on upper portion of canal. Cords at varices becoming five to seven sharp spines extending beyond margin of varix. Varical spines adaperturally oriented. Shoulder spine formed by first primary cord below suture and adapically oriented. First and third spines below suture on varix usually weak to sub-obsolete. Second cord below suture forming periphery of whorl. Aperture narrowly ovate with six low denticles on adaxial margin of outer lip and a deep anal sulcus formed by a single, large denticle on posterior portion of columella. Aperture white. Siphonal canal restricted from body whorl, long, narrowly open. Shell color maroon with darker coloration over axial nodes.

Holotype: BMNH (Not found: Kathie Way, 1998, personal communication).

Type locality: “San Blas, Mexico. In seven fathoms, among mud.”

Occurrence: Fossil: Age unknown (possibly Late Miocene or Early Pliocene), Arroyo Grande at Usiacuri, Dept. Atlantico, Colombia (UCMP loc. S-7607); Early Pliocene, Jama Formation, Puerto Jama, Ecuador (*vide* Vokes, 1989a); Early to middle Pleistocene, Armuelles Formation, Neily, Costa Rica (Pacific side). Recent: San Blas, Mexico to Panama.

Habitat: Offshore (80–300 m) on mud and sand bottom.

Discussion: *Eupleura pectinata* is a distinctive species with its long, constricted siphonal canal, fan-shaped varices, varical spines, and the stark contrast of its solid maroon shell and white aperture. Within the last 30 years, all specialists working on the molluscan fauna of the eastern Pacific, including specialists of the Muricidae, have recognized *E. pectinata* as a distinct taxon.

The fully developed rachidian tooth of the radula of *Eupleura pectinata* (Figures 59–61) is also distinctive and lacks the sharply defined marginal denticles observed in other *Eupleura* and ocenebrine species. A single, sharply defined denticle is present in the nascent region of the rachidian (Figure 61) but disappears rapidly as the radular teeth become increasingly mineralized (Figure 62). A similar phenomenon was reported for several ergalataxine muricids that have more prominent denticles in the juvenile than the adult life history stages (Fujioka, 1985).

This species is taken only rarely from shrimpers' nets in deep water, and few specimens are known. The type locality is at a depth of 14 m, although it is not known whether the type specimen was collected live. Three museum lots represented by live-collected material were found at a depth range of 80 to 300 m.

Vokes (1989a:116) reported a single worn fossil of *Eupleura pectinata* from the Early Pliocene Jama formation of Ecuador (ANSP 15210), although this material could not be found (E. Benamy [ANSP], 1998, personal communication). As of this study, two additional fossil specimens of this species are known. The younger of the two, from the Pleistocene Armuelles Formation of Costa Rica (Pacific side), is a large shell with well-developed rugae on the columella (Figure 56). The second specimen, from the early Neogene of Colombia (Atlantic side), is also large but lacks rugae (Figure 57). The age of this second shell is unknown; although there are numerous fossiliferous outcrops of the Lower Tubará group very near where this specimen was collected on the Arroyo Grande in Usia Curi, Colombia that are thought to be Late Miocene to Early Pliocene in age (Jung, 1989:239–241).

Vokes (1989b) argued that the Early Pliocene species *E. lehneri* is ancestral to *E. pectinata*, although *E. pectinata* also share numerous morphological characters with the Middle to Late Miocene species *Eupleura thompsoni*. Morphologically, all three species resemble one another in having six, widely-spaced, finger-like spines that extend beyond the margins of the varices, an upturned spine on each varix formed by the second spiral cord anterior to the suture, and a smooth shell surface. Traits *E. pectinata* shares with *E. thompsoni* but not *E. lehneri*, however, include a bulbous body whorl, adaperturally curved rather than straight varical spines anterior to the shoulder spine, rib-like rather than web-like varices, a narrowly ovate aperture, node-like rather than sub-obsolete inter-varical axials, a more extensive parietal shield, a more sloped sub-sutural ramp on all spire whorls, a longer and

more constricted siphonal canal, and more reclined axial lamellae and weaker spiral cords on the earliest teleoconch whorls. Although variable, the varices of *E. pectinata* and *E. thompsoni* also often have a weaker and shorter second spine (formed by third spiral cord) anterior to the suture and longer spines above and below (Figures 58, 70). In contrast, the second spine on the varices of *E. lehneri* is often the longest and most developed (Figures 18–20). The primary differences between *E. pectinata* and *E. thompsoni* are the weaker intervarical nodes, smaller aperture, and more aligned varices in the former species.

Eupleura plicata (Reeve, 1844)

(Figures 64–67)

Ranella plicata REEVE, 1844a, 138. REEVE, 1844b, pl. 7, sp. 33. KOBELT, 1878, 139, pl. 38a, fig. 2.

Eupleura muriciformis Broderip, TRYON, 1880, pl. 39, fig. 504.

Eupleura muriciformis var. *curta* ARNOLD, 1903, 249, pl. 8, fig. 9; GRANT & GALE, 1931, 714.

Description: “Shell oblong, somewhat *Murex*-shaped; whorls rounded, rough, longitudinally plicated, noduled around the middle; livid olive-colour, encircled round the middle with a narrow white zone; columella smooth, canal long” (Reeve, 1844a).

Revised description: Shell of moderate size for genus with most shells 30 to 35 mm. Spire whorls cylindrical, wide in diameter. Last teleoconch whorl flattened dorsoventrally. Protoconch unknown. Teleoconch of eight whorls in adult specimens. Early teleoconch whorls tabulate, low, with strong axial lamellae and spiral sculpture. Twelve to fourteen axial elements on all whorls. On penultimate whorl, axial elements forming two varices with five or more varical ribs between varices. Intervarical axial elements on last whorl becoming elongate nodes or sub-obsolete. Varices low, rounded, attached to previous whorl at suture only. Two or three varices on shell beginning at juncture of penultimate and final whorl. Earliest varices thin, low, blade-like, and difficult to distinguish from axial lamellae. Spiral sculpture on early whorls consisting of three strong cords of equal strength. Eight primary cords on body whorl. Several closely spaced cords on canal. Second primary cord anterior to suture strong on spire whorls forming periphery; same cord weak on last teleoconch whorl, and periphery of last whorl formed by third cord anterior suture. Numerous secondaries between primaries. Aperture broadly ovate with six low denticles on inside of outer lip. Siphonal canal not long, bent to the left, and slightly recurved. Shell surface scabrous. Shell color dark brown, reddish-brown, or white. Most shells brown with single white band near periphery.

Holotype: UMCZ I.100.275 (J. Saul Collection), height 34.2 mm, diameter 20.0 mm.

Type locality: “———?” (Reeve, 1844a).

Occurrence: Fossil: Early Pliocene, Sacaco Basin, southern Peru (see below); Pleistocene, San Pedro Series of San Pedro, California. Recent: El Salvador to Peru.

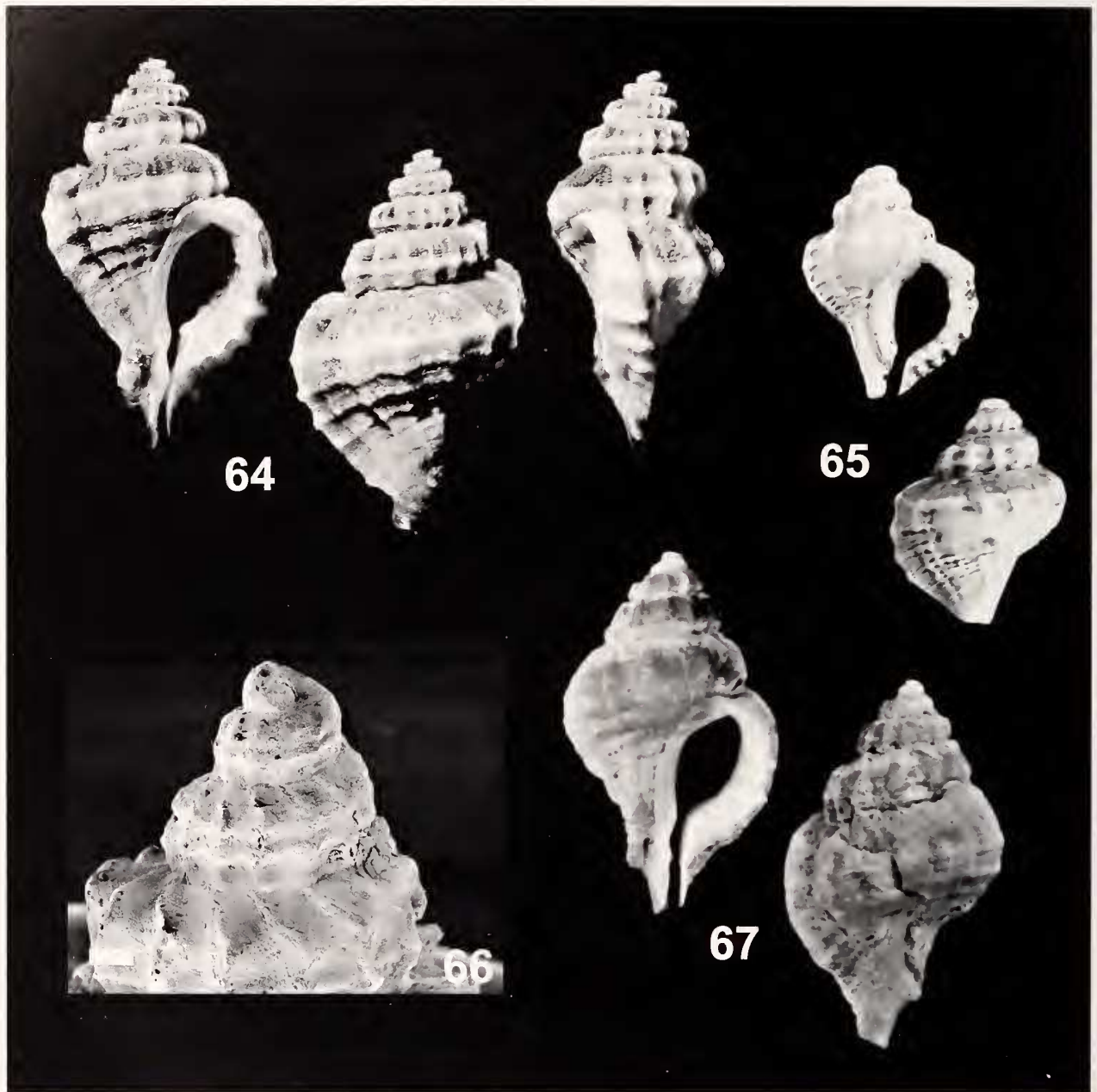
Habitat: Unknown.

Discussion: The holotype of *Eupleura plicata* has been regarded as a variant of *Eupleura muriciformis* with more rounded varices (Keen, 1971) or simply a mutilated siphonal canal (Dall, 1890a). Because of its extreme rarity and often poor preservation in museum collections, no radulae or protoconchs were available for study. Most museum specimens of this species are occupied by dead hermit crabs indicating that few collections of this species, if any, are based on live collected material.

A series of shells studied from several collections show consistent differences between it and other eastern Pacific species. *Eupleura plicata* is most similar to *Eupleura muriciformis* and *Eupleura triquetra* in having a dark brown shell color and white spiral band at the shoulder and in lacking a columellar knob. *Eupleura plicata* differs from *E. muriciformis* and *E. triquetra* in having more cylindrical spire whorls, a less sloped subsutural ramp on the spire whorls, a more sloped subsutural ramp on the final teleoconch whorl, rounded rather than V-shaped varices, more reticulated spiral and axial ornamentation, a more scabrous shell surface, smaller size, five or six rather than three or four intervarical nodes, and a shorter and slightly bent siphonal canal (Figures 64–67). *Eupleura plicata* is thus recognized herein as a distinct species.

The fossil record of *Eupleura plicata* is poor. Arnold (1903) described *Eupleura muriciformis* var. *curta* from the Late Pleistocene San Pedro Series of California, the holotype (Figure 65) of which is identical in size, shape, and sculpture to juvenile *Eupleura plicata* and is clearly synonymous with this species. Interestingly, the northernmost point in the Recent geographic range of *E. plicata* as recorded in museum collections is El Salvador. Arnold's Pleistocene California example implies substantial geographic range contraction during or since the Pleistocene.

Recently collected specimens of what appears to be *Eupleura plicata* from the Early Pliocene Sacaco Basin of southern Peru were recently brought to my attention by T. J. DeVries (personal communication, January 2004). The specimens, which will be described and illustrated elsewhere (DeVries, submitted), are approximately 10 mm smaller than typical mature *E. plicata* and have three rather than five or six intervarical ribs. Other morphological features, however, including the low, rounded varices, complex spiral sculpture, and general shell shape, appear to conform to the general description of *E. plicata*. Because similar variation in



Figures 64–67. *Eupleura plicata* (Reeve, 1844). Figure 64. UMCZ 1.100.275, J. Saul Collection (Holotype); locality: unknown (fide Reeve, 1844a); height 34.2 mm, diameter 20.0 mm. Figure 65. USNM 162559 (Holotype of *Eupleura muriciformis* var. *curta* Arnold, 1903); locality: San Pedro, California; Pleistocene, Upper San Pedro Series; height 15.0 mm, diameter 10.0 mm. Figure 66. ANSP 115981; locality: Archipelago de las Perlas, Panama; scanning electron micrograph of the early teleoconch whorls (scale bar = 200 μ m). Figure 67. UF 267562; locality: Archipelago de las Perlas, Panama; height 35.5 mm, diameter 21.0 mm.

intervarical number and size occurs within other species of *Eupleura*, such as *Eupleura muriciformis*, I tentatively regard the Peruvian fossils as conspecific with *E. plicata* pending further study. Regardless, these Peruvian shells and the modern *E. plicata* are clearly end members of a single lineage.

Eupleura prenitida Vokes, 1989

(Figure 52)

Eupleura prenitida VOKES, 1989b, 119, pl. 1, figs. 1–4.

Description: “Shell small, seven teleoconch whorls in

adult; protoconch unknown. Spiral ornamentation on earliest teleoconch whorls of two cords, a third partially covered by suture. Gradually secondary threads intercalated, until body whorl has approximately ten major cords, best seen on abapertural sides of varices, with between each pair, three to five secondary threads; another six faint threads on siphonal canal. Axial ornamentation on earliest teleoconch whorls of approximately 12 lamellae, diminishing in number and becoming more like axial ridges until about fifth teleoconch whorl two develop into varices, two per whorl, with three strong intervarical nodes between each pair. Varices not well-aligned on opposite sides of the shell, a marked offset between varices on succeeding whorls of as much as 30 degrees. Varices scalloped by extensions of the spiral cords, forming short spines, that at the shoulder are directed adapically. Apertural face of the varices consisting of multiple laminae enfolded into grooves formed by the spiral cords, giving a lacinated appearance to the varical face. Shell surface between the varices also marked by numerous axial growth lines that cause shell material to be drawn out adaperturally where the spiral threads are crossed, giving the entire shell surface a lacinated appearance. Aperture elongate-oval; inner lip adnate, with numerous faint rugae reflecting the underlying spiral cords; margin of outer lip reflected abaperturally, crenulated by grooves of spiral cords; inner side with six strong denticles located between the spiral cords. Siphonal canal moderately long, straight, almost closed over but open by a narrow slit" (Vokes, 1989b).

Holotype: USNM 445390, height 31.1 mm, diameter 17.7 mm.

Type locality: TU 958, Gatun Formation, hill-slope on east side of road from Boyd-Roosevelt Highway to Refineria Panama, S. A., about 0.5 km north of junction, just east of Cativa, Province of Colón, Panama.

Occurrence: Late Miocene, Lower Gatun Formation, Atlantic Panama.

Discussion: According to Jonathan Todd (2002, personal communication), *Eupleura prenitida* is confined to the Lower Gatun Formation of Panama, which represents a "very shallow water" facies, and is replaced higher in the Lower and Middle Gatun by deeper water elements, including *Eupleura thompsoni*. The fact that *E. prenitida* most closely resembles the modern intertidal species *Eupleura nitida*, and *E. thompsoni* most closely resembles the modern deepwater species *Eupleura pectinata* is consistent with ecological restriction across an onshore-offshore sequence rather than chronological restriction.

Vokes (1989b) considered *Eupleura prenitida* to be an evolutionary intermediate between *Eupleura kugleri* and *Eupleura nitida* based on the scabrous shell surface shared by *E. prenitida* and *E. nitida* (Figure 50). Although *E. prenitida* closely resembles both species in

overall shape, size, and sculpture, *E. prenitida* differs from *E. kugleri* and *E. nitida* in having three rather than four or five intervarical axial elements, axial elements forming small rounded nodes rather than elongate ribs between the varices, a longer siphonal canal, unaligned rather than aligned varices on the spire, and a more rounded than V-shaped outline of the varix. The scabrous shell surface texture may actually be a byproduct of growth in an intertidal habitat in which small increments are deposited daily during periodic submersion. Deep water species of *Eupleura*, such as *Eupleura pectinata* and *Eupleura vokesorum*, sp. nov. have completely smooth shells.

Eupleura thompsoni Woodring, 1959

(Figures 68–72)

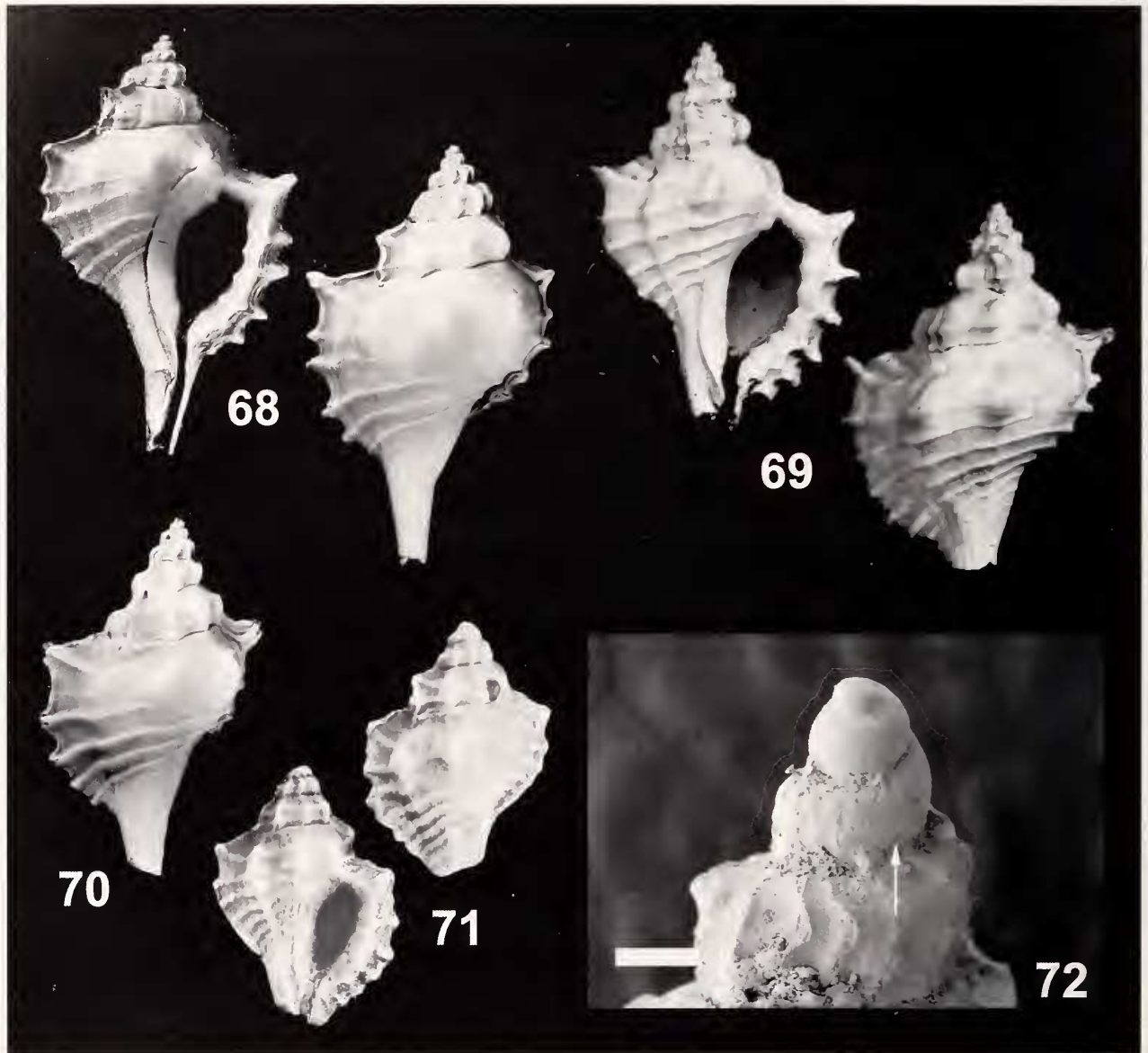
Eupleura thompsoni WOODRING, 1959, 218–219, pl. 36, figs. 6–9.

Eupleura thompsoni Woodring, VOKES, 1989b, 119, pl. 1, figs. 6–8.

Description: "Relatively large, strongly inflated, distinctly but not strongly shouldered. Protoconch blunt-tipped, 2½-whorled, smoothly tapering; a narrow spiral thread at anterior suture on last 1½ whorls. First post-protoconch whorl sculptured with narrow axial lamellae—the first strongly arcuate, the others moderately arcuate—and two low spiral cords. Lamellae slightly overlapping last protoconch whorl. Lamellae gradually widening, but remaining as sharp-edged lamellae up to first varix, which appears on penult or preceding whorl of mature shells. Two varices to a whorl, almost directly opposite each other, but each one later than corresponding varix on preceding whorl. Original lamellae transformed between varices into low swollen ribs, not reaching posterior suture and on body whorl disappearing below periphery. Three or four ribs between varices, generally three, and invariably three between last two varices of mature shells. A rib between early varices rarely has a lamellar edge of outer shell material. Body whorl of mature shells sculptured with seven main spiral cords, the posteriormost faint between last two varices, and as many as five somewhat narrower spiral threads on pillar, fading out anteriorly. Posteriormost spiral cord forming short spine on outer lip; others forming blunt spines or projections; spines generally more or less broken. Interior of outer lip bearing six strong denticles well within aperture. Siphonal canal moderately long, narrow, slightly bent backward; tip broken. Next to last varix forming low lamella on siphonal fasciole" (Woodring, 1959).

Holotype: USNM 562587, height 45.7 mm, 29.5 mm.

Type locality: Gatun Formation, north side of Transisthmian (Boyd-Roosevelt) Highway, knoll about 30 m north of highway, 1.2 km northwest of Sabanitas, Province of Colon, Panama (= Woodring locality 136A).



Figures 68–72. *Eupleura thompsoni* Woodring, 1959. Figure 68. USNM 445395; locality: hill-slope on east side of road from Boyd-Roosevelt Highway to Refinería Panama, S. A., about 0.5 km north of junction, just east of Cativá, Prov. of Colón, Panama; Late Miocene, Gatun Formation (= TU 958); height 34.6 mm, diameter 21.0 mm (Photographs courtesy of E. Vokes). Figure 69. CAS 60191; northwest of Sabanita, Prov. of Colón, Panama; Late Miocene, Gatun Formation; height 37.7 mm (incomplete); diameter 26.5 mm. Figure 70. USNM 445394; locality: same as for Figure 68; height 27.6 mm, diameter 16.9 mm (Photographs courtesy of E. Vokes). Figure 71. UF 91995; locality: Todos Santos, Baja California, Mexico; Late Miocene, Salada Formation (= USGS M 9037); height 17.1; diameter 12.9. Figure 72. NMB H 18153; locality: Prov. of Colón, Panama; Late Miocene, Gatun Formation; scanning electron micrograph of protoconch and early teleoconch whorls (Scale bar = 200 μ m).

Occurrence: Middle Miocene, Salada Formation, Baja California Sur, Mexico; Late Miocene, Lower (?), Middle, and Upper Gatun Formation, Panama; unnamed Late Miocene deposits of Atlantic Colombia and Venezuela.

Discussion: Although previously reported only from Late Miocene deposits in Panama and Colombia, *Eupleura thompsoni* first occurs in the Middle Miocene Salada For-

mation near Todos Santos on the Pacific side of Baja California Sur, Mexico (USGS loc. M9037). J. T. Smith (1991) noted that the Salada Formation contains many deep water and openly neritic mollusks with Caribbean affinities, and the remarkable similarity of this species to the modern *Eupleura pectinata*, which lives at depths from 80 to 300 m, is consistent with these observations.

Another new locality for this species is an unnamed Late Miocene deposit in Venezuela (UCMP S-8338).

Eupleura triquetra (Reeve, 1844)

(Figures 73–82)

Rauella muriciformis Broderip var., SOWERBY, G.B. JR., 1841, pl. 88, fig. "11*."

Rauella triquetra REEVE, 1844b, pl. 7, sp. 41. REEVE, 1844a, 139.

Eupleura muriciformis (Broderip), TRYON, 1880, 158, pl. 39 fig. 505.

Eupleura muriciformis var. *pleistocenuensis* ARNOLD, 1903, 248–249, pl. 9, fig. 16.

Eupleura muriciformis var. *unispinosa* DALL, 1890a, 146.

Eupleura (var?) *unispinosa* DALL, 1891, 174, pl. 6, fig. 5.

Eupleura triquetra (Reeve), RADWIN & D'ATTILIO, 1976, 117, pl. 19, fig. 1.

VOKES, 1984, pl. 2, fig. 21. HERBERT, 2002, 15–16, figs. 1–2.

Description: "Shell elongately Murex-shaped, varices pointed at the upper part; whorls angulated, tubercled at the angle, smooth above, obsoletely ridged beneath; livid olive-colour; columella smooth; canal rather long; aperture small; lip scarcely denticulated" (Reeve, 1844a).

Revised description: Shell fusiform, large for genus. Average shell height approaching 40 mm, maximum shell height near 60 mm. Protoconch of 1.5 whorls. Teleoconch with eight or nine whorls. Early teleoconch whorls tabulate with 12–14 axial lamellae and strong spiral sculpture. Final whorl with eight axial elements, including two varices and three intervarical nodes. Interspiral nodes prominent, horizontal. Spiral sculpture on early whorls consisting of two to three strong spiral cords of even strength. Spiral sculpture on later whorls weak to subobsolete. Secondaries sometimes present. Spire height and slope of sub-sutural ramp variable. Most whorls sloped and with periphery formed by third cord anterior to suture. Up to six varices on shell. Varices offset, moderately expanded, thickened. Shoulder cord at varix forming adapically recurved spine. Remaining cords on varix ending flush with margin of varix but also recurved. Aperture broadly ovate, porcellanous white. Apertural denticles low, six in number; stronger in juveniles. Shell surface usually chalky due to thick, grey intritralx. Worn shells showing brown or dark purple base color and spiral banding of white, or white with brown spiral bands. Siphonal canal long, gently recurved, and narrowly open. Inside of canal brown to purple in color. Spire usually heavily eroded.

Lectotype (here designated): BMNH Reg. No. 1967661/2 (H. Cuming Collection), height 46.9 mm, diameter 24.8 mm.

Paralectotype A: BMNH Reg. No. 1967661/1 (H. Cuming Collection), height 47.0 mm, diameter 25.2 mm.

Paralectotype B: BMNH Reg. No. 1967661/3 (H. Cuming Collection), height 45.3 mm, diameter 23.9 mm.

Type locality: "San Diego, California" (probably an error).

Occurrence: Fossil: Late Pleistocene deposits, San Pedro and San Diego, California and Baja California, Mexico. Recent: Cabo San Lucas, Baja California Sur, Mexico and entire Gulf of California except in vicinity of San Felipe and El Golfo de Santa Clara, Mexico.

Habitat: Intertidal to 5 m on mud.

Discussion: This species is highly variable in size, color and banding patterns, and spire morphology. Mature specimens can range from 35 to more than 60 mm in height; the color of the shell can be dark brown or purple with wide, white bands below the shoulder, or white with a purplish hue and with wide bands of light brown; some specimens are solid orange; many, however, have a thick, scabrous intritralx and appear light grey in color; the spire may be tabulate with axial lamellae and strong spiral ornamentation, or it may have a strongly sloped shoulder with axial nodes and obsolete spiral ornamentation. The early teleoconch whorls are usually heavily eroded; when present, the early whorls of the spire are dark purple in color. Varices on the spire are offset by up to 40 degrees from varices on subsequent whorls, and varices on the last teleoconch whorl are separated from one another by up to 230 degrees, which is greater than in any other species of *Eupleura*. Also unique to *Eupleura triquetra* is the occurrence of three secondary cords between the suture and the shoulder of the body whorl (Figure 80); other species of *Eupleura* have only one. The morphology of the radula of *E. triquetra* (Figures 75–77) is unlike any other species in the genus and appears to be a highly derived form (see previous discussion under *Eupleura limata*).

A lectotype for *Eupleura triquetra* is designated here to clarify the identity of this species, which has been confused in the literature with *Eupleura limata*, *Eupleura muriciformis*, and *Eupleura vokesorum*, sp. nov. The lectotype selected is one of three shells in the type lot in the BMNH and is the shell originally figured by Reeve and Tryon. The lectotype (Figure 74) is easily distinguished from the other syntypes in shell dimensions, which are given above, as well as in having an incomplete lip and a darker shell. Paralectotype A is also figured (Figure 73).

The egg capsules of *Eupleura triquetra*, described and illustrated elsewhere (Herbert, 2002), share the general characters of the Ocenebrinae as outlined by D'Asaro (1991). However, they lack the lateral projection that resembles a secondary mucoid plug in the subtropical and temperate western Atlantic species of *Eupleura*. Furthermore, the *E. triquetra* capsules are more rounded in shape than those of the western Atlantic species, which are generally triangular, and more closely resemble those of the

ocenebrine muricid *Pteropurpura festiva* (Hinds, 1844) figured by D'Asaro (1991). Communal egg masses, consisting of several hundred capsules laid by multiple females, occur in *E. triquetra*, but this strategy is not present in the western Atlantic species of *Eupleura*, which do not spawn communally and rarely produce egg masses larger than ten to 20 capsules (MacKenzie, 1961; Herbert, personal observation).

In Cholla Bay and Estero Morúa near Puerto Peñasco, Sonora, Mexico, *Eupleura triquetra* is common but patchily distributed. In Cholla Bay, the animals may be found at low tide buried in sand with only the tip of the siphonal canal showing. Many were feeding while buried. Prey encountered included the gastropod *Cerithium* (*Theridium*) *stercusmuscarum* Valenciennes, 1833, and the bivalve *Chione undatella* (Sowerby, 1835). Both were attacked by drilling. In Estero Morúa, *E. triquetra* was encountered on intertidally exposed oyster reefs, where it was observed drilling the oyster *Saccostrea palmula* Carpenter, 1857, and on the adjacent intertidal mudflats, where it was observed drilling *C. stercusmuscarum* and an unidentified barnacle attached to these ceriths. In the lab, *E. triquetra* feeds readily on the bivalves *Chione undatella* from its native habitat and *Protothaca staminea* (Conrad) collected from San Francisco Bay. However, its preferred prey are barnacles.

Radwin & Hemingway (1976) reported this species from the Recent of Todos Santos Bay, on the outer coast of Baja California near the California-Mexico border. This occurrence is anomalous since *Eupleura triquetra* does not occur anywhere between this point and the southern tip of Baja California, Mexico near Cabo San Lucas. Radwin and Hemingway suggested that this species may have been introduced with oysters, although this remains unsubstantiated. Interestingly, the type lot from the H. Cuming collection is said to be from "San Diego," which is farther north than the Radwin and Hemingway material but was collected prior to the introduction of oysters. I have found no other records of this species from this area in the hundreds of lots I examined, and the Cuming record is most likely an error. *Eupleura triquetra* has also been reported as far south as Panama (Radwin & D'Attilio, 1976:117), but in all the collections examined, I found only a single lot from Panama and no representative localities between Topolobampo in central Mexico and the Panama locality. The Panama locality is, there-

fore, also probably an error. This species' present range is probably restricted to the Gulf of California, the Cortez Province of Reid (2002), and along the outer coast of Baja California only as far north as Cabo San Lucas.

The Pleistocene fossil taxon *Eupleura muriciformis* var. *pleistocenensis* Arnold, 1903, is referable to *Eupleura triquetra* as are nearly all of the Pleistocene *Eupleura* fossils from southern California and Baja California, Mexico. Fossil *Eupleura* reported in the literature as *Eupleura muriciformis* from Pleistocene deposits of San Diego (Hertlein & Grant, 1944) and Newport Bay, California (Kanakoff & Emerson, 1959) and Turtle Bay, Baja California Sur (Chace, 1956; Emerson, 1980) were determined to be *E. triquetra* after study of the large Pleistocene collections from this region in the LACMIP and UCMP collections.

Other aspects of this species are discussed above under *Eupleura limata* and *Eupleura muriciformis*.

Eupleura vokesorum Herbert, sp. nov.

(Figures 83–89)

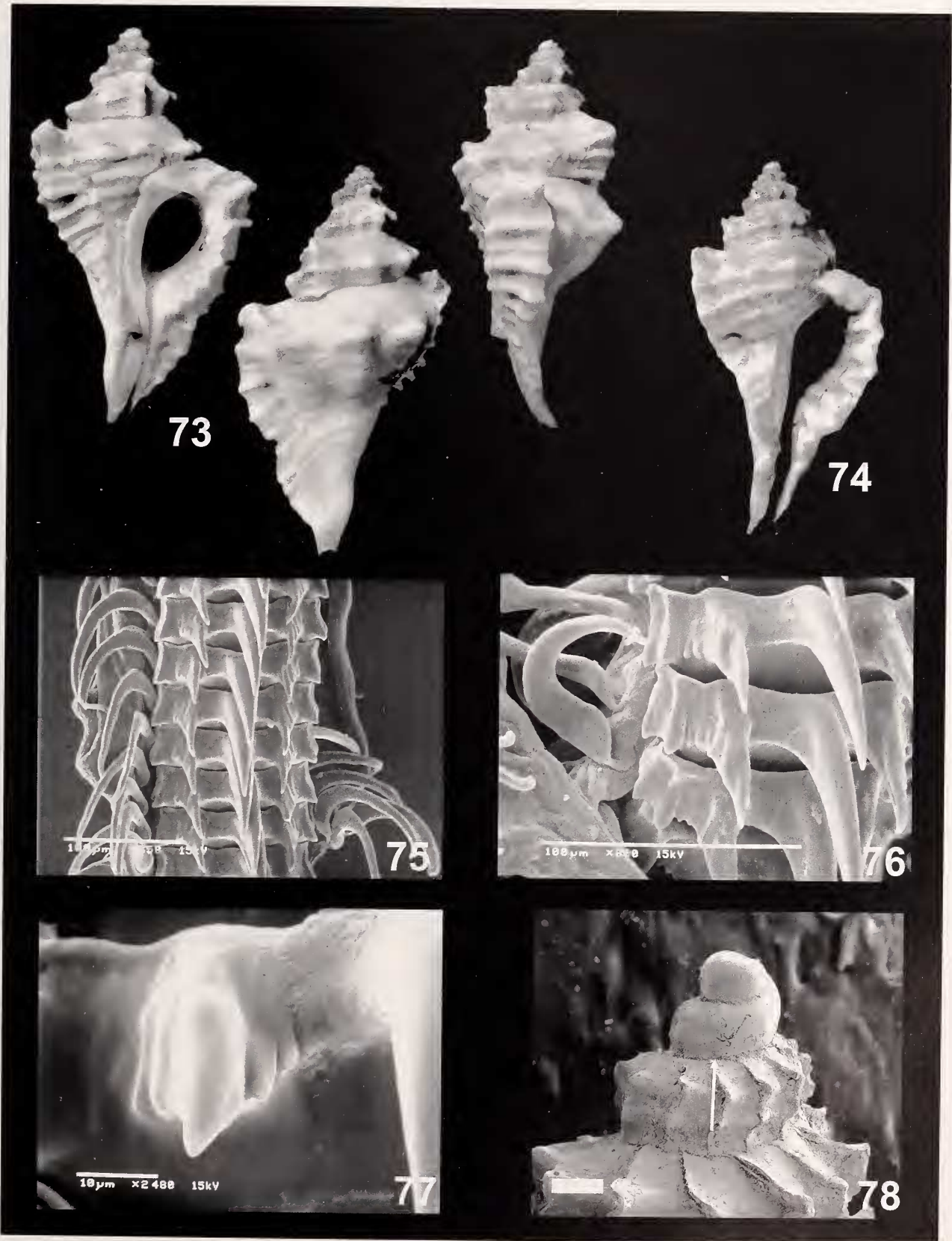
Eupleura muriciformis (Broderip), DALL, 1890a, 145. DALL, 1890b, 174, pl. 5, fig. 2. SMITH, M. 1944, 25, fig. 307. ABBOTT, 1974, 188, fig. 1961. KEEN, 1971, 530, no. 1024. RADWIN & D'ATTILIO, 1976, 115–116, pl. 19, fig. 5. VOKES, 1984, pl. 2, fig. 19.

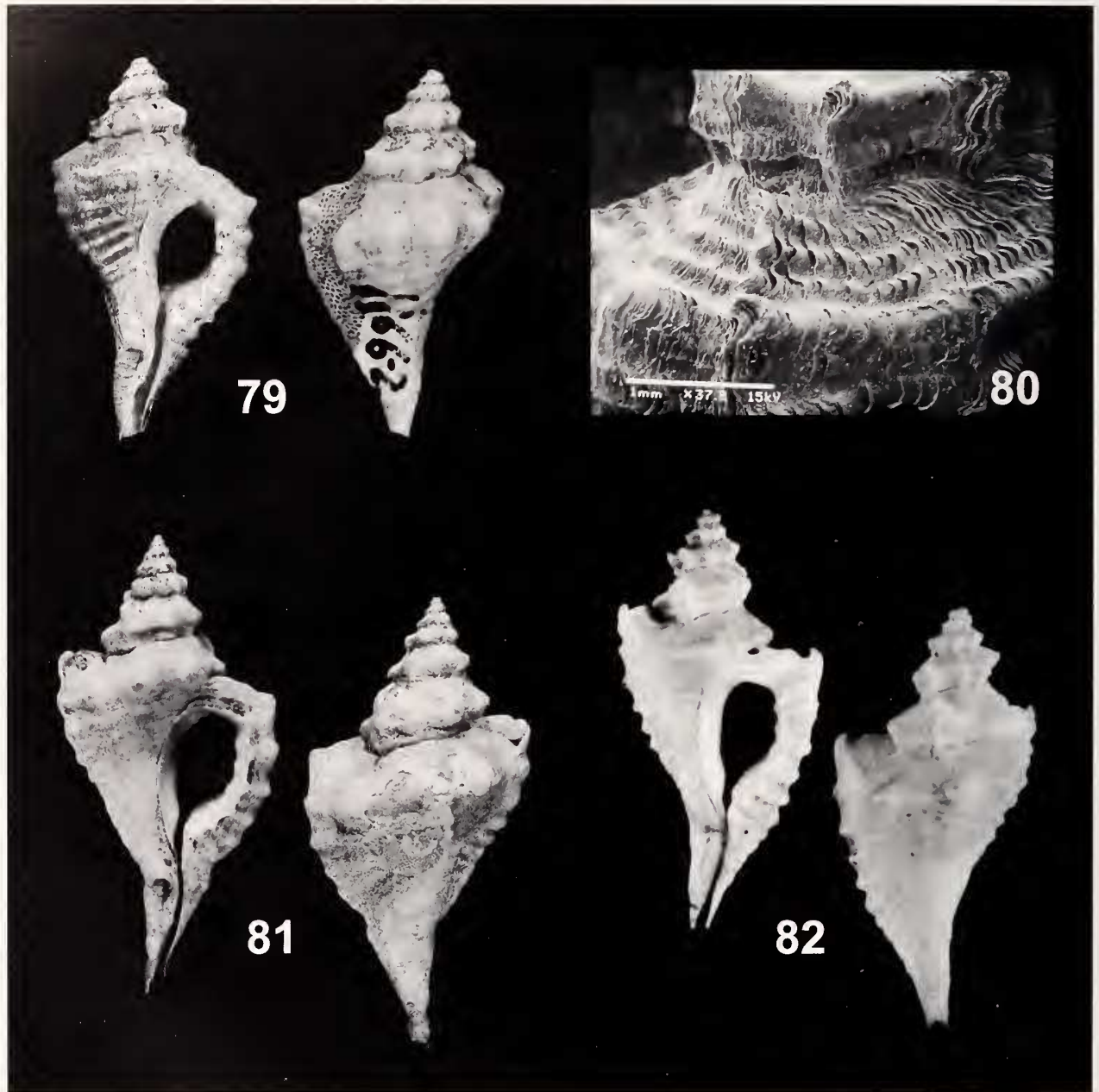
Diagnosis: As for *Eupleura muriciformis*, but with three rather than four intervarical nodes, smooth rather than crispate shell surface, less adapically directed shoulder spines, smaller aperture, higher spire, more sharply defined shoulder and fewer axial lamellae on early teleoconch whorls, weaker spiral ornamentation on adapical portion of the body whorl, and solid maroon shell color rather than banded white and brown.

Description: Shell large for genus; trigonal in shape. Maximum height to approximately 50 mm but averaging around 30–40 mm. Teleoconch with eight or nine whorls; protoconch of 2.5 rounded, glossy whorls. Spire high, with narrow, scalariform early teleoconch whorls; later whorls becoming more sloped. First teleoconch whorl tabulate with no spiral sculpture; subsequent early whorls have one cord forming well-defined shoulder. Later teleoconch whorls with one sub-obsolete cord between suture and shoulder, six sub-obsolete to moderate cords widely

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Figures 73–78. *Eupleura triquetra* (Reeve, 1844). Figure 73. BMNH Reg. No. 1967661/1, H. Cuming Collection (Paralectotype A); locality: "San Diego, California" (probably an error, see text); height 47.0 mm, diameter 25.2 mm. Figure 74. BMNH Reg. No. 1967661/2, H. Cuming Collection (Lectotype); locality: same as Figure 73; height 46.9 mm, 24.8 mm. Figures 75–77. LACM 34123; locality: El Coyote Bay, Mexico; scanning electron micrographs of the radula (scale bar = 100 μ m in Figures 75, 76; scale bar = 10 μ m in Figure 77). Figure 78. LACM 59-7; locality: Empalme, Sonora, Mexico; scanning electron micrograph of the protoconch and early teleoconch whorls (scale bar = 200 μ m; arrow points to protoconch/teleoconch transition).





Figures 79–82. *Eupleura triquetra* (Reeve, 1844). Figure 79. LACMIP 7163; locality: Newport Beach, California; Late Pleistocene, Palos Verdes Sand; height 32.2 mm, diameter 16.9 mm. Figure 80. Scanning electron micrograph of the spiral sculpture within the subsutural ramp (Scale bar = 1 mm). Figure 81. LACM 71-29; locality: intertidal, La Paz, Baja California, Mexico; height 42.7 mm, diameter 21.0 mm. Figure 82. USNM 2636 (Holotype of *Eupleura muriciformis* var. *unispinosa* Dall, 1890); locality: Mazatlan, Gulf of California, Mexico; height 36.2 mm, diameter 18.0 mm.

spaced on body whorl and four closely spaced cords on upper portion of canal. Periphery of whorl formed by third cord anterior to suture on late teleoconch whorls. Cords at varix form sharp spines that extend beyond varix margin. Shoulder spine elongate, straight, with abapical orientation; body spines shorter, sharply and abaperturally recurved. Axial ornamentation on early whorls consisting

of eight to ten axial lamellae. Two varices on later whorls separated by three prominent nodes. Four to six varices present on shell; first varix forms on fifth or sixth whorl. Varices offset slightly from previous whorl. Varices bladelike, expanded. Aperture ovate, small, with six weak denticles on outer lip; lowermost two denticles occasionally fused. Two very weak denticles across top of aper-

ture, columellar lip smooth, and one cord-like denticle on the posterior portion of columellar wall formed by fifth cord from suture on underlying whorl. Siphonal canal long, straight to slightly recurved, and narrowly open. Shell color solid maroon.

Holotype: UCMP 198998, Guaymas, Mexico, height 39.8 mm, diameter 25.7 mm.

Paratype A: USNM 519551, Pliocene, Costa Rica, height 22.4 mm (incomplete), diameter 15.3 mm.

Paratype B: UCMP 198999, Guaymas, Mexico, height 40.6 mm, diameter 31.9 mm.

Type locality: Recent, Guaymas, Mexico.

Etymology: This species is named for Emily and the late Harold Vokes in honor of their contributions to the systematics of western Atlantic mollusks.

Occurrence: Fossil: Pliocene, Vaca Formation, Puntarena Province, Costa Rica. Early Pliocene, Jama Formation, Ecuador (see below). Late Pliocene, Canoa Formation, Ecuador (see below). Recent: San Felipe, Mexico to Punta Aji, Colombia.

Habitat: Offshore (20 to 200 m) on mud and sand bottom.

Discussion: *Eupleura vokesorum*, sp. nov. is a common species in the museum collections examined, although it has been identified until now as the less common *Eupleura muriciformis*. In addition to major differences in depth of habitat, opercular shape, and radulae, the two species are easily separable on the basis of shell features alone. These are discussed in detail above under *E. muriciformis*. Affinities to fossil species are also discussed under *Eupleura olssoni*.

The only confirmed fossil occurrence for this new species is based on two shells from Pliocene deposits from the Puntarena Province of Costa Rica (Figure 84). Additional Pliocene material from the Punta Jama and Punta Canoa formations of Ecuador (ANSP 15210), identified as *Eupleura muriciformis* by Vokes (1989a:116, footnote), is probably *Eupleura vokesorum*, sp. nov. based on my understanding of Vokes' concept of *E. muriciformis*, which was illustrated in Vokes (1984) and exemplified in her private collection (personal observation). Unfortunately, the ANSP lot could not be found (E. Benamy, 1998, personal communication).

DISCUSSION

This study of the fossil and Recent *Eupleura* of tropical America revises the stratigraphic and/or geographic ranges of eight species, resurrects two species from previous synonymy, and describes four new species. As a result, the Pliocene diversity of *Eupleura* species in the tropical western Atlantic is increased fivefold, the Recent diver-

sity of the group in the tropical eastern Pacific is nearly doubled, and several of these living eastern Pacific species are shown to have an extensive and previously undocumented fossil record that includes early Caribbean occurrences. While these additions substantially improve our understanding of the history of this genus, their greater impact for understanding the history of the tropical American biota as a whole can only be fully appreciated as basic taxonomic monographs on additional groups are completed and the species-level database for the region is updated.

Faunal Exchanges between the Atlantic and Pacific Oceans

These revised data on species occurrences through time and space shed light on biogeographic patterns of invasion and speciation for *Eupleura*. Five of the seven living tropical eastern Pacific species are geologically old (>4 Ma), and at least three of these four occur first in the fossil record of the tropical western Atlantic prior to entering the tropical eastern Pacific. Final closure of the Panamanian Seaway is thought to have occurred sometime between 3.5 and 3.1 Ma (Keigwin, 1982; Duque-Caro, 1990), although several studies have suggested that closure was intermittent throughout the Pliocene (Coates et al., 1992; Collins et al., 1996; Cronin and Dowsett, 1996), and that faunal exchange still occurred as late as the Early Pleistocene (1.8 to 0.7 Ma) during interglacial periods of elevated sea-level (Beu, 2001). The fossil record of *Eupleura* in tropical America is consistent with these observations.

Faunal exchanges between the Atlantic and Pacific for *Eupleura* occurred intermittently from the Miocene through perhaps the earliest Pleistocene. The progenitor of the genus, *Eupleura kugleri* from the Early Miocene (23.8 to 16.4 Ma) of the southern Caribbean, was followed in the Middle to Late Miocene (16.4 to 5.32 Ma) with records of the genus from both sides of the Isthmus. *Eupleura thompsoni*, which occurred only in the eastern Pacific during the Middle Miocene, occurred on both sides of the Isthmus by the Late Miocene. *Eupleura pectinata* occurred on both sides of the Isthmus in the Pliocene (5.3 to 1.8 Ma) but became restricted to the eastern Pacific after the Pliocene. New fossil records of the modern eastern Pacific species *Eupleura muriciformis* show that this species occurred in the tropical western Atlantic from the Middle Miocene to the Late Pliocene and in the tropical eastern Pacific from the Late Pliocene onwards. The most recent evidence of a faunal connection between the Atlantic and Pacific *Eupleura* faunas is *Eupleura utida*, which is known from fossil deposits of Early to middle Pliocene (5.3 to 2.6 Ma) age in the tropical western Atlantic and in the Early to Middle Pleistocene (1.8 to 0.1 Ma) of the tropical eastern Pacific.

Pliocene Mass Extinction in the Tropical Western Atlantic

Marine communities of the western Atlantic region experienced a regional mass extinction event in the Pliocene, with losses of roughly 70% of species living in that time and restrictions of many surviving lineages to extinction refuges in the southern Caribbean and eastern Pacific (Petuch, 1981, 1982, 1995; Vermeij and Petuch, 1986; Allmon et al., 1996b; Jackson, 1993, 1996; Roopnarine, 1996). Analyses of the timing and patterns of extinction are continuing but point decidedly towards a Pliocene reduction in nutrient levels and collapse of communities dependent upon planktonic production as a primary cause of the extinctions (Allmon et al., 1996a). The existence of upwelling conditions where Pliocene relicts survive to this day (Petuch, 1982) and a shift from eutrophic to oligotrophic micro- and nanofossil communities throughout the Caribbean in the Pliocene (McDougall, 1996; Bornmalm et al., 1999; Kameo, 2002) are consistent with these observations.

The ecology of *Eupleura* species suggests an inherent susceptibility to such an event. Although its species do not have planktotrophic larvae, members of this genus are carnivorous and feed predominantly on suspension- and filter-feeding organisms, such as barnacles and bivalves (MacKenzie, 1961; Radwin and Wells, 1968; Herbert, this paper).

The diversity of the genus *Eupleura* in the Caribbean collapsed from a high of five species in the Late Miocene through the Early Pliocene to only one or two species in the Late Pliocene. A second extinction in the Caribbean resulted in the loss of any remaining surviving lineages of *Eupleura* at the end of the Late Pliocene. Extirpation of the genus from the Caribbean was, thus, stepwise and complete. Three of the five Early Pliocene Caribbean species, however, survive today in the eastern Pacific, suggesting that broad geographic range and fortuitous occurrence of populations in the eastern Pacific permitted some lineages to survive.

Post-Pliocene Diversification in the Eastern Pacific

Two of the seven living eastern Pacific species of *Eupleura*, *Eupleura limata* and *Eupleura triquetra*, are geologically young (Pleistocene to Recent or Recent only)

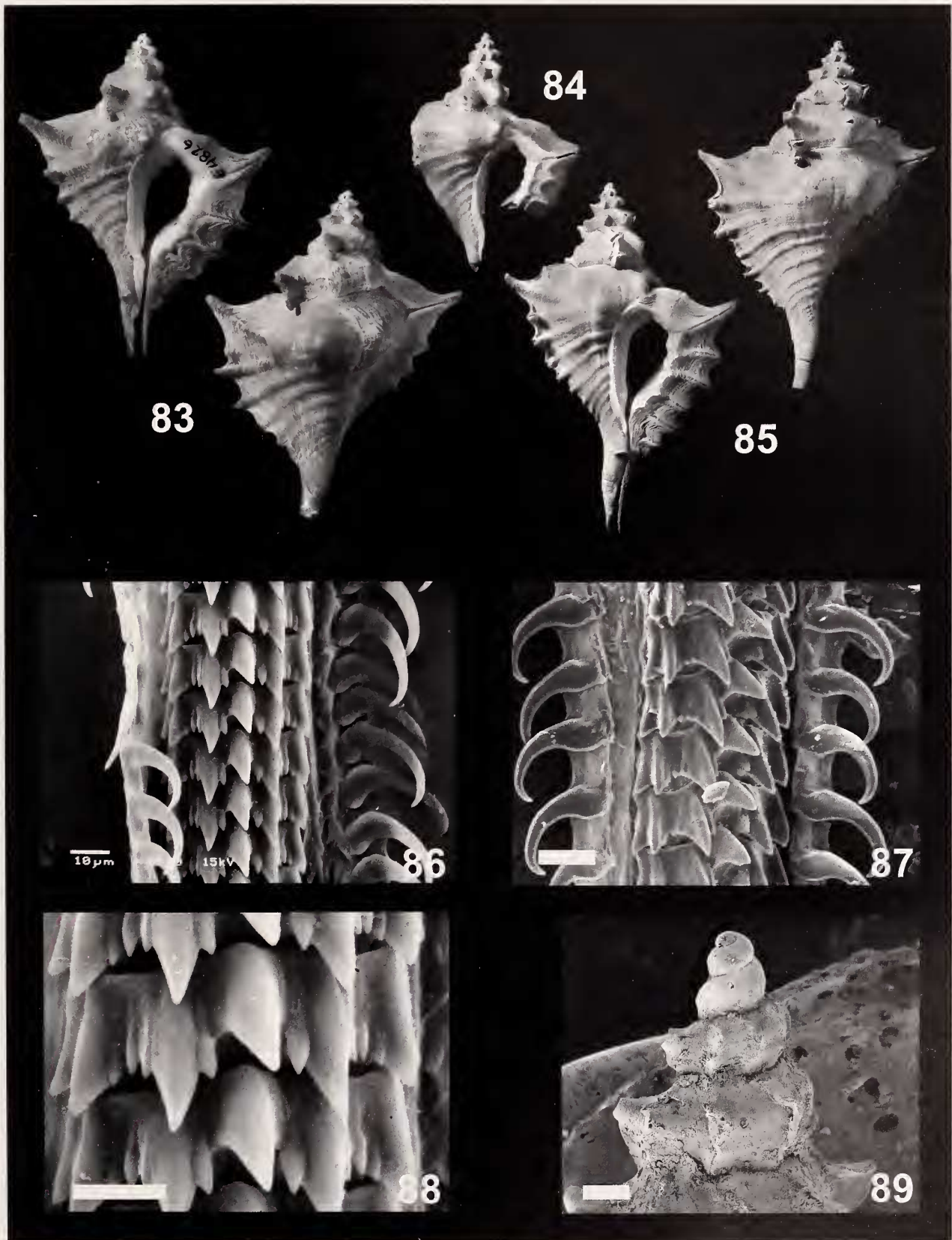
relative to other members of this genus in the eastern Pacific. Interestingly, both are restricted to the Gulf of California today, and one (*E. triquetra*) first occurs as a Pleistocene fossil in this region. In contrast, all five of the geologically older eastern Pacific taxa (the Middle Miocene to Recent *Eupleura muriciformis*, the Early Pliocene to Recent *Eupleura nitida*, the Late Miocene or Early Pliocene to Recent *Eupleura pectinata*, the Early Pliocene? to Recent *E. plicata*, and the Early Pliocene to Recent *Eupleura vokesorum*) are restricted to the region from southern Mexico to Peru or extend well into this area. Thus, most of the Pleistocene and recent diversification of the genus in the eastern Pacific has been restricted to the Gulf of California rather than being evenly distributed throughout the geographic range of the genus.

One possible factor that may explain this difference in speciation potential is depth of habitat. Neither of the geologically younger species has been found living in waters deeper than 15 m, whereas many of the geologically older species regularly occur in water deeper than 25 m. One of these, *E. pectinata*, has been collected at depths of 300 m. Reid (2002) noted that some speciation in the Littorinidae of the eastern Pacific has been associated with the formation of gaps in suitable rocky coast and mangrove habitats. Pleistocene climate change, which altered drainage patterns along the west coast of the Americas (Dalrymple & Hamblin, 1998; Guerro et al., 1999) and therefore local salinities and substrates in coastal areas, is one mechanism that may explain the differential speciation potentials of shallow water and deep water species. Additional tests comparing divergence times in closely related shallow and deeper water taxa are needed.

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Figures 83–89. *Eupleura vokesorum* Herbert, sp. nov. Figure 83. UCMP 198999 (Paratype B); locality: Guaymas, Mexico; height 40.6 mm, diameter 31.9 mm. Figure 84. USNM 519551 (Paratype A); locality: Stream courses, including Río Vaca, near eastern part of trail, from Progreso (in Panama near Costa Rican border) to Lagarto (on Golfo Dulce), Puntarena Province, Costa Rica; Early Pliocene, Vaca Formation (= USGS reg. no. 24792); height: 22.4 mm (incomplete), diameter 15.3 mm. Figure 85. UCMP 198998 (Holotype); locality: Guaymas, Mexico; height 39.8 mm, diameter 25.7 mm. Figures 86–88. LACM 111193; locality: Chamela Bay, Jalisco, Mexico; scanning electron micrographs of the radula (scale bar = 10 μ m in Figures 86–88). Figure 89. Herbert collection: Guaymas, Mexico; scanning electron micrograph of the protoconch and early teleoconch whorls (scale bar = 200 μ m).



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